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A BIOPHYSICAL APPROACH TO MODELING ELEVATIONAL RANGE SHIFTS IN COLORADO MAMMAL COMMUNITIES

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Abstract

Species geographic ranges are shifting in the face of contemporary climate warming, and documenting range shifts is crucial to our understanding of the underlying drivers mediating movement in geographic range limits. Studies on elevational range shifts with climate change are beginning to accrue within the literature, though observed shifts are idiosyncratic and difficult to predict. Some species may respond to warming temperatures by shifting their range limits upslope, where temperatures are cooler owing to the adiabatic lapse rate. However, species may also respond to warming temperatures in an elevation-dependent manner: if changes in snow depth expose overwintering organisms to colder air temperatures, they could shift upwards, where snowpack is deeper, or downard, where air temperatures are warmer. Physiological tolerance is often cited as a major driver of species distributions, but studies rarely connect organismal physiology to changes in climate and concomitant shifts in species' elevational ranges. Even fewer studies focus on the factors governing elevational range shifts in mammals at the seasonal scale. Advances in the field of biophysical ecology allow for the direct translation of changes in environmental conditions over time to currencies directly relevant to organismal fitness. Here, we apply mechanistic models of heat flux to test whether changes in thermoregulatory costs underlie observed range shifts in 41 species of small mammals in the Colorado Rocky Mountains. We gathered biophysical and behavioral data on focal species from museum specimens and the literature, and quantified microhabitat conditions with high-resolution forcing data and newly-developed microclimate models. We calculated the change in both cooling and heating costs at historical range limits across the past century to test whether changes in thermoregulatory requirements drove movement at both lower and upper elevational range limits. Overall, changes in thermoregulatory costs did not explain elevational range shifts in our system. Mammals largely decreased heating costs, and increases in cooling costs were negligible. Changes in thermoregulatory costs varied across seasons and elevation. Our results suggest that movement at elevational limits in small mammals is largely driven by other abiotic and biotic factors rather than thermoregulatory costs alone. We submit that future research on the drivers of elevational range shifts in mammals would benefit from a more holistic and nuanced approach, rather than focusing solely on changes in the physiological costs of thermoregulation.

Keywords
Range shifts, thermoregulatory costs, mammals, snow, Colorado Rockies, climate change, biophysical ecology, mechanistic models

INTRODUCTION

Climate Change provides a chance to better understand range-limiting factors

All over the globe, shifting climates continue to disrupt local ecosystems and increase extinction risk (Inouye et al. 2000; Urban 2015). One way in which ecosystems are affected by changing climates is through the redistribution of species across the landscape (Colwell et al. 2008; Sinervo et al. 2010; Parmesan & Yohe 2003). As temperature regimes shift, some organisms may no longer be able to tolerate parts of their historical range (Colwell & Rangel 2009). For organisms that cannot meet the ensuing challenges with behavioral adjustments, phenotypic flexibility, or rapid evolution, dispersal to more favorable microclimates provides the only avenue from extirpation (Travis et al. 2013; Hallfors et al. 2023). Forecasting where and when populations will move is of great interest to biologists (Thuiller et al. 2008; Dawson et al. 2011; Schurr et al. 2012); however, different levels of warming necessarily lead to unique expectations for local communities and their predicted degrees of range shift (Loarie et al. 2009). Uncovering the fundamental drivers governing range shift responses to climate change would greatly benefit our understanding of why we find organisms where we do on the landscape.

Predicting range shifts is obscure

Documenting range shifts is crucial to our understanding how biotic communities have responded to contemporary climate change (reviewed in Tingley et al. 2009). One strategy for quantifying range shifts is through the use and resurvey of historical occurrence data, either from museum collections, field notes, or both (Shaffer et al. 1998). Studies of this kind are beginning to accrue within the literature (Moritz et al. 2008; Rowe et al. 2010; Rowe et al. 2015; Crimmins et al. 2011; Buckley & Kingsolver 2012; McCain & King 2014; McCain et al. 2021). However, identifying general rules that govern which species shift their ranges–and by how much–has proven to be a multifaceted and elusive problem. Though some studies find select organismal traits to be useful predictors of species-level responses to climate change, others fail to find strong relationships using the same traits in different systems (reviewed in Bessienger & Riddell 2021). A meta-analysis of 8,653 range shifts across 42 species assemblages demonstrated that for seven commonly-reported traits (body size, migratory strategy, dispersal ability, fecundity, longevity, diet breadth, and habitat breadth), none showed strong relationships to species range shifts (Maclean & Beissenger 2017). Beissenger & Riddell (2021) remark that "*while traits may show effects in individual studies, overall their effects and importance are inconsistent across studies, making them problematic indicators of species' range responses to future climate change.*"

Uncovering the drivers of species' range shifts is further obscured by the fact that both abiotic and biotic factors, as well as their interactions, can influence range shift patterns in diverse taxa (Sexton et al. 2009). For example, Ewards (2004) showed that contractions at the southern range limit in giant kelp (*Macrocystis pyrifera*) were related to high temperatures and wave activity after an extreme weather event, and kelp were unable to recolonize their formerly-occupied habitat due to competition with other species that were unaffected by disturbance. Further, *Clarkia xantia*–a plant endemic to California–experience decreased pollinator visitation and increased pollen limitation at their range edge, suggesting plant-pollinator dynamics partially govern the range limits in this species (Moeller et al. 2012). In this way, species may be prevented from shifts into suitable habitats by the absence of suitable hosts and mutualisms, but also the presence of competitors and predators (HilleRisLambers et al. 2013). The convergence of both biotic and abiotic influences may help to explain the lack of any single predictive variable in determining range shifts across species.

New tools to investigate range shifts – the promise of biophysical models

The most commonly used approaches to describe distributions and range limits are correlative species distribution models (Elith & Leathwick, 2009). These models identify statistical relationships between species occurrence and predictor environmental variables (Briscoe et al. 2022), and have proved useful in a variety of ecological contexts (Dormann et al. 2012). However, correlative approaches make implicit assumptions about the underlying processes actually governing range shift responses, and thus limited in their biological realism and transferability to novel environments (Loehle & Leblanc 1996; Davis et al. 1998). There is strong evidence that physiological tolerance to climatic factors dictate the location of geographic range margins in diverse taxa (Sexton et al. 2009; Cahill et al. 2013), but studies often assume that species' range shifts are influenced by concomitant changes in climate without explicitly linking temperature change to physiology (Moritz et al. 2008; Rowe et al. 2009; Rowe et al. 2015; Mamantov et al. 2021; McCain & King 2014; Walther et al. 2002; McCarty 2001). Moreover, such studies assume observed range shifts are connected to contemporary changes in climate, without knowledge of how species' ranges varied prior to anthropogenic climate change (Nogues-Bravo et al. 2018). Our inference of the drivers of species range shifts is hampered without consideration of the mechanisms actually linking species to their local environments (Kearney & Porter 2009).

One potential solution is to use mechanistic biophysical models (e.g., heat flux simulations) to integrate across suites of traits related to energy and water balance (Bessienger & Riddell 2021). A recent uptick in the usage of biophysical models in the literature reflects a growing need to incorporate mechanism into models of species' range shifts (Briscoe et al. 2022). The real boon of these models is that, unlike correlative approaches, they focus on the limiting processes–such as mass and energy flow–that determine where organisms can persist using the fundamentals of biophysical ecology (Gates 1980; Kearney & Porter 2009). The focus of most biophysical modeling to date is on ectotherms, though the usage of endotherm models is growing (reviewed in Briscoe et al. 2022). Biophysical approaches translate changes in environmental conditions over time into currencies directly relevant to the fitness of the organism in question, making them ideal tools to for attributing observed range shifts to changes in climate (Riddell et al. 2019; Riddell et al. 2021; Briscoe et al. 2021; Dormann et al. 2012).

An important consideration when employing biophysical models is the accuracy of the model output. Realism must be built into biophysical models via the characterizations of the organisms themselves, but also through proper descriptions of their local microenvironment (Pincebourde & Woods 2020). Recent developments in microclimate modeling provide a user-friendly method for downscaling gridded macroclimate data for use in individual-based biophysical modeling (Kearney & Porter 2017; Kearney 2020). Apart from quantifying an organism's habitat, biophysical simulations can also incorporate differences in how organisms use the microenvironments available to them. In reality, an organism's habitat is a mosaic of climatic heterogeneity, and topographical features (eg. tree cover, underground burrows) that enable rapid toggling of the microclimate an organism experiences in any given moment (Chappell & Bartholomew 1981). That animals can experience dramatically different temperature regimes over short spatial and temporal scales necessitates the integration of animal behavior into biophysical approaches (Kearney et al. 2021; Riddell et al. 2019; Riddell et al. 2021).

Mountains provide refuge from warming climates, but maybe not from winter cold

The usage of biophysical models is still in its infancy with regard to climate change and its influences on range shifts (Briscoe et al. 2022). For example, only a handful of studies to date have applied biophysical simulations of heat flux to organisms living in mountainous ecoregions (Moyer-Horner et al. 2015; Mathewson et al. 2017), and none of them have used heat flux simulations to link observed elevational range shifts with changes in thermoregulatory costs. Apart from harboring high rates of biodiversity (Körner and Spehn 2019), mountains provide rapid relief from rising temperatures compared to changes in latitude. On average, temperatures decrease by ~6°C for every 1000 m of elevation gain; in contrast, that same decrease in temperature occurs over ~1000 km of latitudinal change (Colwell et al. 2008). As the climate continues to shift, communities distributed along elevational gradients may track their thermal niches through time and space by migrating upslope (Pauli et al. 1996). Indeed, there is evidence that this phenomenon is already occurring in diverse taxa as lower elevations warm and force communities upwards (Parmesan & Yohe 2003; Moritz et al. 2008; McCain et al. 2021; Rowe et al. 2015).

But climate change may also mediate range shifts in unintuitive ways as well: a recent study determined that endotherms occupying high-altitude regions of the southern Rocky Mountains are projected to experience greater heating costs as a result of climate change via reductions in snow cover and depth (Kearney 2020). Snow acts as an insulator that buffers the soil surface from vacillations in air temperature (Taylor & Buskirk 1994; Pruitt 1957). Deep snow shields small organisms living in the subnivean zone (underneath the snow) from temperature extremes, such that the snow-soil interface stays close to 0℃ regardless of the air temperature above (Pauli et al. 2013). As a result, organisms living under snow typically experience the coldest temperatures during early autumn and late spring (i.e., the shoulder seasons), before persistent snowpack develops and air temperatures are relatively cold (Slatyer et al. 2021). Communities that rely on snowpack as insulation during colder months could respond to such changes by shifting upwards–where snow is deeper and more persistent–or downwards–where temperatures during the winter tend to be warmer. Approaching this problem across seasons, rather than focusing only on warmer months, may help to explain non intuitive range-shift patterns observed over the past century (Laorie et al. 2009).

Range shifts in Small Mammals

Elevational range shifts in small mammals in particular have proved difficult to predict in this context: studies show high degrees of interspecific variation in the direction of elevational range shifts in recent history (Moritz et al. 2008; Rowe et al. 2015; McCain et al. 2021), a trend that variation in single traits has largely failed to explain (Angert et al. 2011; Moritz et al. 2008; Beissenger & Riddell 2021). Climate-induced thermoregulatory stress also may not affect organisms living across elevational gradients equally: for instance, studies suggest that mid-elevation sites (2591–3048 m) may be experiencing the fastest rates of warming in Colorado (McGuire et al. 2012), and distances moved by species tend to be greatest under higher rates of warming (Chen et al. 2011). A recent study in the Colorado Rockies showed that montane species–or those occupying predominantly mid to high elevations–were more likely to shift their range limits upwards compared to low-elevation and generalist species (McCain et al. 2021). Extinction risk in small, high-altitude mammals may be mediated by increases in air temperature and concomitant increases in energy and water expenditure for thermoregulation (Moyer-Horner et al. 2015; MacArthur & Wang 1973). On the other hand, increases in heating costs due to depletion in snow depth could drive idiosyncratic shifts during colder months of the year (Kearney 2020; Pauli et al. 2013; Slatyer et al. 2021). Most studies examining elevational range shift responses in mammals focus on cooling costs rather than heating costs, and there is great potential to apply biophysical models to uncover the biophysical constraints limiting species' elevational range limits spatially and temporally (Rubidge et al. 2011).

In this study, we endeavored to test the assumption that observed shifts in small mammals' elevational ranges (McCain et al. 2021) are causally linked to changes in thermoregulatory costs, using mechanistic models of heat flux to quantify the magnitude of cost changes through time. Over the past century of climate warming, small mammals in Colorado have moved their elevational ranges upwards by an average of 131 m (McCain et al. 2021). Moreover, cold-adapted species, defined as 1) species with higher elevational range limits, 2) those for whom the study locations occur in the southern portion of their geographic range and 3), species with higher maximum latitudes in their species geographical ranges, shifted their range limits upwards most often (McCain et al. 2021). Movement patterns in this system are attributed to observed increases in temperature, with no real mechanistic link between climate change and elevational range shifts. Like many other studies that have documented range shift responses to climate warming over the past century (reviewed in Rubenstein et al. 2023), some small mammals showed downward elevational shifts or the absence of shifts altogether. The inclusion of changes in thermoregulatory costs in colder seasons could help to elucidate why some species display unexpected responses under a model of climate warming (Williams et al. 2015).

We combine newly-developed biophysical simulations (Riddell et al. 2021; Riddell et al. 2019) with morphological, behavioral, and physiological data collected on 47 different small mammal species from museum collections and the literature. We also take advantage of microclimate models (Kearney & Porter 2017) to downscale high-resolution monthly gridded climate data reaching back to 1895 (Daly et al. 2008). Our approach also captures the interaction between snow cover and soil temperature (Kearney 2020) to evaluate how exposure to climate change influences elevational range shifts in all seasons of the year. Using estimates of elevational range limit change across the past century, we simulated both cooling and heating costs for thermoregulation in small mammal species at their historical range limits, and calculated the change in costs between historical (1895-1924) and contemporary (1992-2020) climate regimes. We used this approach to address the following interrelated hypothesis:

1. Changes in annual thermoregulatory costs at historical range limits drive species' elevational shifts
2. Increases in cooling costs and heating costs at historical range limits drive range shifts during the summer and shoulder seasons, respectively.
3. Increases in heating costs at historical range limits are greatest for species occupying mid elevations, and those species are more likely to experience elevational range shifts.

METHODS

Mammal Resurveys

Data on historical (1886 to 1979) and contemporary (post 2005) elevational distributions for 47 species ranges were taken from McCain et al. (2021). In brief, historical elevational ranges were built using museum specimen data from 45 different museums. Contemporary data were also collected from museums and supplemented with live-trapping surveys from four elevational transects. Bayesian analyses were used to estimate the probability that an animal was present but undetected due to undersampling within 50 m elevational bins extending from 1400 to 3800 meters in the Front Range (FR) and San Juan (SJ) mountains of Colorado. 95% likelihood elevational ranges were compared between historical and contemporary time periods to detect directional change. Two species, *Sciurus aberti* and *Tamiasciurus hudsonicus*, were excluded from our analysis because they are primarily arboreal squirrels that are not known to burrow underground, thus requiring a completely different modeling approach from the other species in the analysis. Further, four species (*Dipodomys ordii, Perognathus fasciatus*, *Perognathus flavus*, *Peromyscus crinitus*) went extinct between the historical and contemporary periods, and were thus excluded from our study. Overall, this left us with 41 species range shifts for downstream analyses (FR, n = 23; SJ, n = 18).

Site Selection & Climate Data

Monthly mean minimum temperature, monthly mean maximum temperature, and monthly total precipitation were obtained from the parameter-elevation regressions on independent slopes model (PRISM, https://prism.oregonstate.edu/). PRISM generates monthly and yearly climate surfaces using mathematical interpolation and expert knowledge (Daly et al. 1994; Daly et al. 2002). With high spatial resolution (~800 m), the PRISM dataset is well suited to climatically variable terrain such as the mountainous regions in this study.

We used monthly variables to compute mean estimates of temperature and precipitation for historical and contemporary eras (1895–1924 and 1991–2020 respectively). The chosen periods represent the most extreme ends of the temporal envelope stipulated by McCain et al. (2021), and encompass the largest degree of temperature change over that period (Frankson et al. 2017). We recognize that the selected time periods do not perfectly match the years included in the construction of the elevational ranges in McCain et al. (2021); however, we believe that if thermoregulatory costs are driving elevation range shifts in this system, those changes should be most apparent when temperature differences between the two focal periods are most extreme (Chen et al. 2011). We gathered climate data for both mountain ranges in Colorado museum specimen data and live trapping surveys were collected by McCain et al. (2021) (FR: Boulder & Larimer counties; SJ: Dolores, LaPlata, Montezuma, & San Juan counties). The GPS coordinates bounding each polygon were built in ArcGIS (v. 10.8.2). We initially hoped to obtain GPS records for each of the specimens used to build each species' elevational range, but these data were unavailable.

To understand how climate varies with elevation in these two regions, we randomly sampled 1000 GPS points between 1400 and 3800 m in each of the two mountain ranges and binned them by elevation (n = 48) using the digital elevation model (DEM) from the PRISM climate group website (https://prism.oregonstate.edu/normals/). We chose 50 m as our binning increment to reflect the resolution of species elevational ranges built in McCain et al. (2021). Land area decreases above the 2,500 m contour; therefore, we limited the sample size of each bin to 28 GPS points, as this number matches the altitudinal band in our polygons with the fewest number of cells according to the DEM. For each bin, we averaged climate data from all 28 GPS points to produce 12 months of temperature and precipitation normals for each elevational bin, mountain range, and time period.

It is important to recognize that our approach ignores the effects of potentially significant micrometeorological variables, such as slope, aspect, and hillshade (Kearney & Porter 2017). However, we assume that these variables have not changed significantly over the past century. Instead, we take a simplified approach that focuses on changes in climate and its effects on changes in thermoregulatory costs for montane mammals across time and altitude (Riddell et al. 2019; Riddell et al. 2021).

Microclimate Modeling

We used NicheMapR (v.3.2.1, Kearney & Porter 2017) to downscale our monthly climate estimates from PRISM and calculate relevant microhabitat conditions for small mammals. In short, the NicheMapR microclimate model simulates hourly conditions at a series of heights above the ground and depths below the snow or soil surface by applying the principles of physics and meteorology to inputted weather station data. We used NicheMapR to generate microhabitat conditions for each elevational bin in both mountain ranges and time periods (n = 192). These conditions were then used to iterate across each species, generating estimates of hourly thermoregulatory costs along an elevational gradient. To simulate microclimates, NicheMapR requires the latitude, longitude, and elevation of each site as input. For each elevational band, we averaged these three variables across all 28 GPS coordinates. We then used these mean locales as input for each elevational bin within the NicheMapR microclimate model.

Snow plays a crucial role in buffering small mammals from changes in ambient temperatures during the winter (Pauli et al. 2013; Kearney et al. 2020) and varies as a function of elevation. To include the effects of snow on thermoregulatory costs of montane mammals, we employed the snow model included in the NicheMapR microclimate suite (described in detail in Kearney et al. 2020). To validate subnivean soil temperatures generated by NicheMapR, we compared predicted and observed values using data from the Snow Telemetry Network (SNOTEL) collected by the Natural Resources Conservation Service (https://www.wcc.nrcs.usda.gov/scan/). Soil temperature data was collected at ten sites in the Rocky Mountain West spanning an elevational gradient from 1,800 to 3,322 m. All available soil temperature data were downloaded from each site for all available depths and summarized to generate average monthly temperatures. We compared these values to our predicted values generated from NicheMapR and the PRISM dataset based upon the coordinates and elevation of the site (Table 1).

Table 1: Validation of the NicheMapR microclimate model at 10 high-elevation SNOTEL sites in the Rocky Mountains using monthly PRISM data as forcing. Mean R-squared, Intercept, and P-values are provided for each modeled soil depth.

Sensor Depth (cm)	**Intercept (α)**	**R^2**	**P**
5	-0.612	0.97	1.34E-07
10	-1.1	0.951	6.60E-08
20	-0.942	0.9656	1.39E-07
50	-0.604	0.956	4.51E-06
100	0.104	0.825	3.25E-04

Behavior & Microhabitats

We incorporated behavior and variation in body temperature (T_b) into our simulations of heat flux. Many small mammal species employ heterothermy (hibernation or daily torpor) to cope with extreme climatic conditions at high elevations in the winter (Geiser 2021; Ruf & Geiser 2015). While there is some evidence that hibernators are emerging earlier in the season under climate change (Wells et al. 2022; Inouye et al. 2000), we assumed that emergence dates remained the same over the past century. For simplicity, we also assume males and females from each species follow the same activity patterns. We defined a normothermic period (May through August), when all species were simulated as defending a body temperature of 37°C, and a heterothermic period (September through April) when heterothermic species were simulated as using daily torpor or hibernation. Heterotherms were assigned species-specific torpor body temperatures (T_{tor}) determined from values in the literature (Kramm 1972; Ruf & Geiser 2015; McNab 1992; Dearing et al. 2008; Wolff & Bateman 1978; Hudson 1962; Morrison 1959; Churchfield 1990; Brigham & Geiser 2012; Cong et al. 2020). For species without data on minimum torpid body temperatures, we used average minimum values across congeners in our dataset.

Species were grouped into four categories based on their thermoregulatory strategies: 1) active mammals, hibernators, 2) daily torpor users, and 4) shrews. Active mammals, or those not known to use heterothermy, were modeled as being normothermic at all times of year. Hibernators were modeled as always being underground during the heterothermic period. Daily torpor users were modeled as being above ground and normothermic during their active states (i.e., during the day for diurnal animals), and underground and torpid when inactive. When torpid, we modeled T_b as equivalent to the operative temperature (T_e, Bakken 1992) from the previous hour. When $T_e < T_{tor}$, we set $T_b = T_{tor}$, thus simulating the defense of minimum body temperatures in the cold (Ruf & Geiser 2015). Thermoregulatory costs were set to 0 when $T_b > T_{tor}$ to mimic passive heating and cooling by the environment (Dausmann et al. 2020). We acknowledge that the control of body temperature is not completely suspended during torpor, even when $T_b > T_{tor}$ (Ambler et al. 2021; Geiser 2004; Humphries et al. 2002). Further, species vary in the degree to which T_b tracks T_a, largely due to differences in size and shape (Porter & Kearney 2009). Nevertheless, our approach dynamically captures the tracking of body temperature with T_e above species-specific thresholds (Geiser & Kenagy 1988), as well as energetic savings that would otherwise be overlooked by assuming a constant minimum T_b during torpor.

Shrews, being unique among our species, are neither diurnal or nocturnal, and are not known to hibernate or use daily torpor (Churchfield 1990). Given their extremely high metabolic rates, shrews must eat frequently throughout the day and night in all seasons or risk starvation (Churchfield 1990; Schaeffer et al. 2020). We modeled shrews as being normothermic year round, and for each hour of the day, shrews were randomly assigned as being above or below ground (Buchalczyk 1972). We ensured that shrews spent equal time in each condition over the course of 24 hours, and matched those conditions spatiotemporally between historical and contemporary simulations to ensure that thermoregulatory differences between eras were not due to differences in the spatial position of the animal.

During periods of inactivity, we assumed that mammals retreated underground to species-specific burrow depths determined by values from the literature (Laundre & Reynolds 1993; Koontz et al. 2001; Van Vuren & Ordenana 2012; Criddle 1915: Gano & States 1982; Racey 1928; Churchfield 1980; Bihr & Smith 1998; Cranford 1978). For species without known burrow depth values, we used average values across the genus. Burrows were modeled to occur at one of the depths exported by NicheMapR (e.g., 2.5, 5, 10, 15, 20, 30, 50, and 100 cm). The lowest possible depth for a burrow was 2.5 cm and the deepest was 1 m. If soil depth was between 2.5 and 5 cm, we modeled the burrow depth at 2.5 cm, using this same protocol for each depth interval of soil. In theory, small mammals could track favorable depths throughout the day such that cooling and heating costs are minimized; however, since some species are nocturnal and generally inactive during the daytime, we concluded that this scenario is unrealistic (Riddell et al. 2021).

Mammal Specimen Data

We amassed specimen data from the Phillip L. Wright Zoological Museum (UMZM) at the University of Montana, supplemented with specimens from the Denver Museum of Nature and Science (DMNS). For simplicity, we restricted analyses to adult rodent and shrew specimens to match the specimens used to build elevational ranges in McCain et al. (2021). Thermoregulation during other life stages may be important in determining where species occur on the landscape (Gong et al. 2023); however, we chose to focus on adult animals to mimic those used in McCain et al. (2021). Given the limited number of specimens at our disposal, we chose to include specimens from across the Western portion of the USA to maximize sample sizes per species (n = 10), endeavoring to represent each sex equally in our measurements. From each specimen, we recorded data on mass, sex (when known), sampling location, sampling elevation, year sampled, and the month sampled. We measured the length of each specimen from the crown to the vent, width from shoulder to shoulder, and height from the back on the dorsal side to the breast at the shoulder using a Fisherbrand™ 150 mm ruler. The length and thickness of the fur on the dorsal and ventral sides of each specimen were also recorded, following the method described by Riddell et al. (2022). In brief, we placed the base of a ruler at the base of the hair and pressed the hair against the ruler to measure the length to the nearest 0.5 mm. We measured the thickness at the same three locations spanning the dorsal and ventral sides of the specimens as the vertical distance from the outer surface of the skin to the outer surface of the hair. The density of the fur can play an important role in the thermal properties of the pelage (Tregear 1965; Wasserman & Nash 1979). We assumed a value of 11,200 fibers/cm^2 from empirical measurements on fur density in small rodents (Sealander 1951), electing not to sample the density of the fur ourselves due to the labor-intensive process. Moreover, differences associated with fur thickness are likely a combination of density and thickness, as they are often correlated (Tregear 1965). We used data on the thermal insulation of mammal pelage from Riddell et al. (2022). For species in which data on the thermal insulation of the pelage were not available, we used mean values from closely related species, or used mean values across all rodents in the analysis. We also estimated solar absorptance of the dorsal and ventral sides of each specimen using empirical data on closely related species (Riddell et al. 2021; Gates 1980).

Heat Flux Simulations

To generate estimates of thermoregulatory costs, we used heat flux simulations designed for use on small mammal communities (see Riddell et al. 2021 for a detailed explanation of the model and validation). Briefly, these simulations use biophysical principles to estimate the rate at which mammals lose or gain heat to their environment based upon:

$$Q = M - E - CdTbdt= ke\ (Tb- Te)$$

where Q is the net sensible heat flux, M is the heat generated through metabolic processes, E is the heat lost via evaporative processes, C is the heat capacitance of the isothermal core, Tb is body temperature, t is time, Ke is the effective conductance, and Te is the operative temperature (Bakken 1981). The model calculates the amount of heat (kJ/day) that an animal must generate through metabolic processes (i.e., thermoregulatory heating costs) or lose through evaporative cooling (i.e., thermoregulatory cooling costs) for every hour of an average day within each elevational bin and era. In select analyses, we also calculated total thermoregulatory costs (heating costs + cooling costs) as an indicator of total thermal stress.

We simulated changes in thermoregulatory costs over the past century for 37 small mammal species to explore the relationship between contemporary climate warming and mammal elevational range changes in the Colorado Rockies. Mammals were modeled at their historical elevational range limit using microclimate data from both time periods to understand how thermoregulatory costs at a species' altitudinal extremes have changed through time. For our analyses, we chose to represent thermoregulatory costs in kJ/day. In analyses requiring the comparison of cost changes between species, we divided kJ/day by mass to correct for the effects of body size on estimates of thermoregulatory costs. We chose to use mass-corrected values rather than use mass as a covariate, as many of our analyses were non-parametric and do not allow for the inclusion of covariates. All Simulations were run in Python (v. 3.11.4) using custom scripts developed by EAR and modified by RTM (Riddell et al. 2019; Riddell et al. 2021).

1. Testing the Relationship Between Changes in Elevational Range Limits and Thermoregulatory

1.1 Continuous analysis

To explore the relationship between elevational range shifts and changes in thermoregulatory costs, we first calculated mass-specific annual thermoregulatory costs for each species at their historical lower elevational limit (LEL) and upper elevational limit (UEL), combining species from the Front Range and the San Juans (n = 41). We then subtracted historical costs from modern costs to yield delta thermoregulatory costs for each species at both elevational range limits. We then related these changes to the direction and magnitude of observed changes in elevational range limits (McCain et al. 2021) using linear regression.

1.2 Movers vs. Non-Movers

To investigate whether thermoregulatory costs increased more for species that shifted their UEL or LEL in either direction, we again calculated mass-specific changes in thermoregulatory cost at each historical range limit for both eras and mountain ranges, subtracting historical values from contemporary values. We performed analyses using both annual and monthly climate data. Next, we grouped species by movement type, designating 'movers' as species that shifted their UEL or LEL by 100 m or more in either direction, and 'non-movers' as species that shifted their UEL or LEL by 50 m or less, following McCain et al. (2021). We then compared the magnitude of changes in thermoregulatory costs between groups with Mann-Whitney U tests to infer whether movers incurred greater changes in costs between the two eras.

1.3 Directional Change

To relate movement direction to changes in thermoregulatory costs, we compared species that shifted their range limits in specific direction with all other movement phenotypes (i.e., those that moved their LEL upwards vs. those that did not move their LEL + those that moved their LEL downwards). Again, we calculated historical and contemporary thermoregulatory costs at historical range limits for all species (n = 41) and calculated the change in costs between periods. Based on the results from the previous analysis, we chose to analyze these data using only monthly delta thermoregulatory costs. Finally, we compared changes in thermoregulatory costs between groups to test whether species shifting their ranges in specific directions exhibited greater changes, or opposite changes, in thermoregulatory costs relative to other species responses with Mann-Whitney U tests.

1.4 Cold-Adapted Species

To understand whether cold-adapted species incurred higher changes in thermoregulatory costs across eras, we ran three separate analyses focusing on 1) elevational affiliation, 2) the maximum latitude of species ranges, and 3) the location of the study areas within species geographic ranges. Trait data were gleaned from McCain et al. (2021). We first grouped species by elevational affiliation (Low: n =21; All: n = 11, Montane: n = 12), and then calculated mass-specific changes in annual thermoregulatory costs for each group as described above. Next, we calculated changes in annual thermoregulatory costs at the UEL and LEL for all species (n = 41) and related those changes to the maximum latitude of their geographic ranges. Finally, we grouped species by the location of the focal mountain range within their geographic range (East: n = 13; Middle: n = 7; North: n = 8; South: n = 10; West: n = 3) and calculated annual changes in cooling costs at the UEL only. We focused solely on changes in the UEL for the first and third analyses, as this was the only elevational limit that significantly shifted upwards in these groups (McCain et al. 2021). For analyses 1) and 2), we used Kruskall-Wallace tests with Benjamini-Hochberg adjustments for multiple testing. For analysis 3), we used linear regression.

2. Community-Wide Changes in Thermoregulatory Costs Across Space and Time

2.1 Cost Change Through Time

To discern how thermoregulatory costs changed over different timescales, we calculated thermoregulatory costs for all species (n = 41) annually and monthly at their historical range limits under both historical and contemporary climates. We then summed costs across all species and compared the magnitude of community-level cost changes through time. We used paired student's T-tests for the annual comparison and ANOVA with Tukey HSD post-hoc tests for the monthly comparison.

2.2 Cost Change Across Elevation

To examine which elevations showed the largest changes in thermoregulatory costs through time, we calculated mass-specific changes in thermoregulatory costs for species across their historical elevational extents. For all species falling within a given 50 m elevational bin, we calculated thermoregulatory costs under historical and contemporary climate regimes, and calculated delta changes by subtracting historical costs from contemporary costs. We then averaged mass-specific changes in thermoregulatory costs across all species in each 50 m bin, and fit splines to relate costs to elevation.

Phylogenetic Analyses

To test for phylogenetic signal in mass-specific heating costs, we used the mammal supertree from Bininda-Emonds et al. (2007). We first pruned the supertree to include only the taxa represented in our dataset. We excluded five species from the analysis (C*allospermophilus lateralis, Ictidomys tridecemlineatus, Microtus mogollonensis, Myodes gapperi, Otospermophilus variegatus*) which are present in our phenotypic dataset but were not present in the tree. Next, we used multi2di() in the R package *ape* v 5.7.1 (Paradis et al. 2004; Paradis and Schliep 2019) to resolve multichotomies and check that the tree is ultrametric. To calculate phylogenetic signal, we used the R package *phytools v 1.9.16* (Revell 2012) to assess significance using Pagel's Lambda (Pagel 1999) and Bloomberg's K (Bloomberg et al. 2003). For both metrics, we found most traits were non-significant; however, we did detect significant phylogenetic signal in delta heating costs at the LEL (Table 2). Phylogenetic signal was non-significant for three of the four traits, and range shifts in our species did not show phylogenetic signal (McCain et al. 2021). As such, we decided to present non-phylogenetically-corrected values.

Table 2: Results from phylogenetic tests on mass-specific delta thermoregulatory costs across all species in the analysis (n = 36). Only heating costs at the LEL showed significant phylogenetic signal.

Phenotype	Lambda	p-value	K	p-value
Δ Cooling Costs LEL	0.208431	0.32929	0.237714	0.1007
Δ Heating Costs LEL *	1.02586	0.00015*	0.624513	0.0029*
Δ Cooling Costs UEL	0.20605	0.308047	0.202481	0.2527
Δ Heating Costs UEL	0.00008	1	0.23993	0.1496

* Indicates significant phylogenetic effect.

Statistical Analyses

All statistical analyses were conducted in R (v. 4.2.3). For our linear regression analyses, we used the *lm* function from the *stats* package (v. 4.2.3). We employed Mann-Whitney U tests using the *wilcox.test* function to account for non-normal distributions, Kruskall-Wallace tests with Benjamini-Hochberg adjustments for multiple testing using the *kruskal.test()* function, and paired student's T-tests using the *t.test()* function. For the ANOVA, we used the *aov()* function, and used a Tukey HSD post-hoc test with the *TukeyHSD()* function from the *stats* package. Finally, we fit splines with the *geom_smooth()* function in ggplot2 using the '*loess*' method.

RESULTS

1. Do changes in thermoregulatory costs explain community-wide changes in elevational range limits?

1.1 Annual comparison

To determine how changes in thermoregulatory affect elevational range shifts, we simulated species at their historical LEL and UEL under both historical and contemporary climate regimes, and then subtracted historical costs from contemporary costs. We performed a continuous analysis relating these changes in thermoregulatory costs at the annual scale to the direction and magnitude of elevational range shifts for species in both mountain ranges (n = 41). Overall, we found no relationships between elevational range shifts and changes in thermoregulatory costs (R^2= 0.038, p = 0.22; R^2= 0.056, p = 0.14; R^2= 0.00012, p = 0.95; R^2= 0.0021, p = 0.77; Fig. 1A, B, C, D).

1.2 Changes in thermoregulatory costs between movement phenotypes

To determine whether general movement phenotypes were related to changes in thermoregulatory costs, we grouped species based on two different shift patterns at elevational limits: 1) we expected that species that shifted their ranges (i.e., movers vs non-movers) would have greater changes in thermoregulatory costs compared to species that did not move; 2) we predicted species that shifted their elevational limits in specific directions (i.e., species moving their LEL upwards vs species moving their LEL downwards & species not moving their LEL) would exhibit opposing changes in thermoregulatory cost. We calculated thermoregulatory costs at historical range limits under historical and contemporary climate regimes, and then subtracted contemporary costs from historical costs while correcting for the effects of mass. We performed analyses using both annual and monthly climate data to explore whether seasonal effects might drive range shift patterns.

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Using annual changes in thermoregulatory costs, regardless of direction, we found that only heating costs at the LEL were significantly different between movement phenotypes, and the group with greater decreases in heating costs was the group that did not move its LEL (p = 0.03103; Fig. 2B). Analyzing the same groups with monthly data, we found significant differences in heating costs between movers and non-movers at the LEL in March (p = 0.02), May (p = 0.04), and October (p = 0.0032; Fig. S1A; Table S1), and differences in cooling costs in September (p = 0.0034; Fig. S1B; Table S1). In all cases, the group that did not change their elevational limit between eras showed greater increases in cooling costs and greater decreases in heating costs. Similarly, in our analysis of movement direction, the only significant difference between groups was at the LEL in the month of September (p = 0.048), where the group that shifted their LEL upwards only displayed marginal decreases in heating costs over time, whereas the group that did not move its LEL upwards showed a greater decrease in heating costs (Fig. S2, Table S2).

1.3 Changes in thermoregulatory costs and range shifts for cold-adapted species

McCain et al. (2021) showed that cold-adapted mammals were 75% more likely to move their UEL up in elevation in our study system. To understand whether changes in thermoregulatory costs drove this pattern, we analyzed mass-corrected annual changes in costs at the historical UEL for mammals according to 1) their elevational affiliation (Armstrong et al. 2011), 2) the maximum latitude of their geographic range, and 3) the position of the focal mountain ranges within their geographic distribution. Each of these variables represent significant predictors of upward migration in Front Range and San Juan mammal communities (McCain et al. 2021). We hypothesized that montane species, species with ranges reaching higher latitudes, and species simulated at the southern edge of their geographic range, would exhibit the greatest changes in thermoregulatory costs. Contrary to these predictions, we found that changes in annual cooling costs at the historical UEL increased the most for low-elevation species (p = 0.0009; Fig. 3A), while changes in heating costs were the same among groups (p = 0.2066 Fig. 3B). Further, species that were simulated at the southern edge of their geographic range did not show greater changes in thermoregulatory costs compared to other groups (p = 0.2782; p = 0.7630; Fig. 3C, D). Finally, we found no significant relationship between changes in thermoregulatory costs and the maximum latitude of species' geographic ranges (R^2 = 0.017, p = 0.42; R^2 = 0.035, p = 0.24; Fig. 3E, F).

2. Are changes in thermoregulatory costs greater during the summer and shoulder seasons?

To determine how thermoregulatory costs have changed over the past century of climate warming, we simulated species at their historical LEL and UEL under both historical and contemporary climate regimes, and then subtracted historical costs from contemporary costs. We predicted that the greatest increase in cooling costs would occur during the summer, and the greatest increases in heating costs would occur during the shoulder seasons (Spring and Fall). Annually, we found that at both elevational limits, cooling costs increased by a community-wide average of ~ 0.5 kJ/Day and heating costs decreased by ~ 2 kJ/Day (p = 0.0013; p < 0.0001; p = 0.002; p < 0.0001; Fig. 4A, B, D, E). In our monthly analysis of changes in thermoregulatory costs, we found that the greatest increases in cooling costs, as well as the greatest decreases in heating costs, occurred during the summer months of June, July, and August (p < 0.0001; p < 0.0001; Fig. 4C, F). However, the largest percentage of species displaying increases in heating costs occurred during the Fall at the LEL (November, 48.8%; Table S3) and Spring at the UEL (April, 36.6%; Table S3).

3. Do changes in thermoregulatory costs at mid-elevations drive range shifts?

To understand where costs have changed the most across elevations, we calculated mass-specific cooling and heating cost changes at historical range limits, averaging values across species occurring within each 50 m elevational bin. We hypothesized that increases in cooling costs would be greatest at mid to high elevations (2591–3048 m), where temperatures are predicted to increase the most in Colorado (McGuire et al. 2012). Again contrary to our predictions, our analysis showed that the greatest increases in cooling costs occurred at lower elevations in both mountain ranges (Fig. 5A, B). Heating costs decreased the most at mid-to-high elevations in both mountain ranges (~3000 m; Fig. 5A, B). Finally, historical range limits at mid elevations were not more likely to shift their range limits (p = 0.28; Fig. S3).

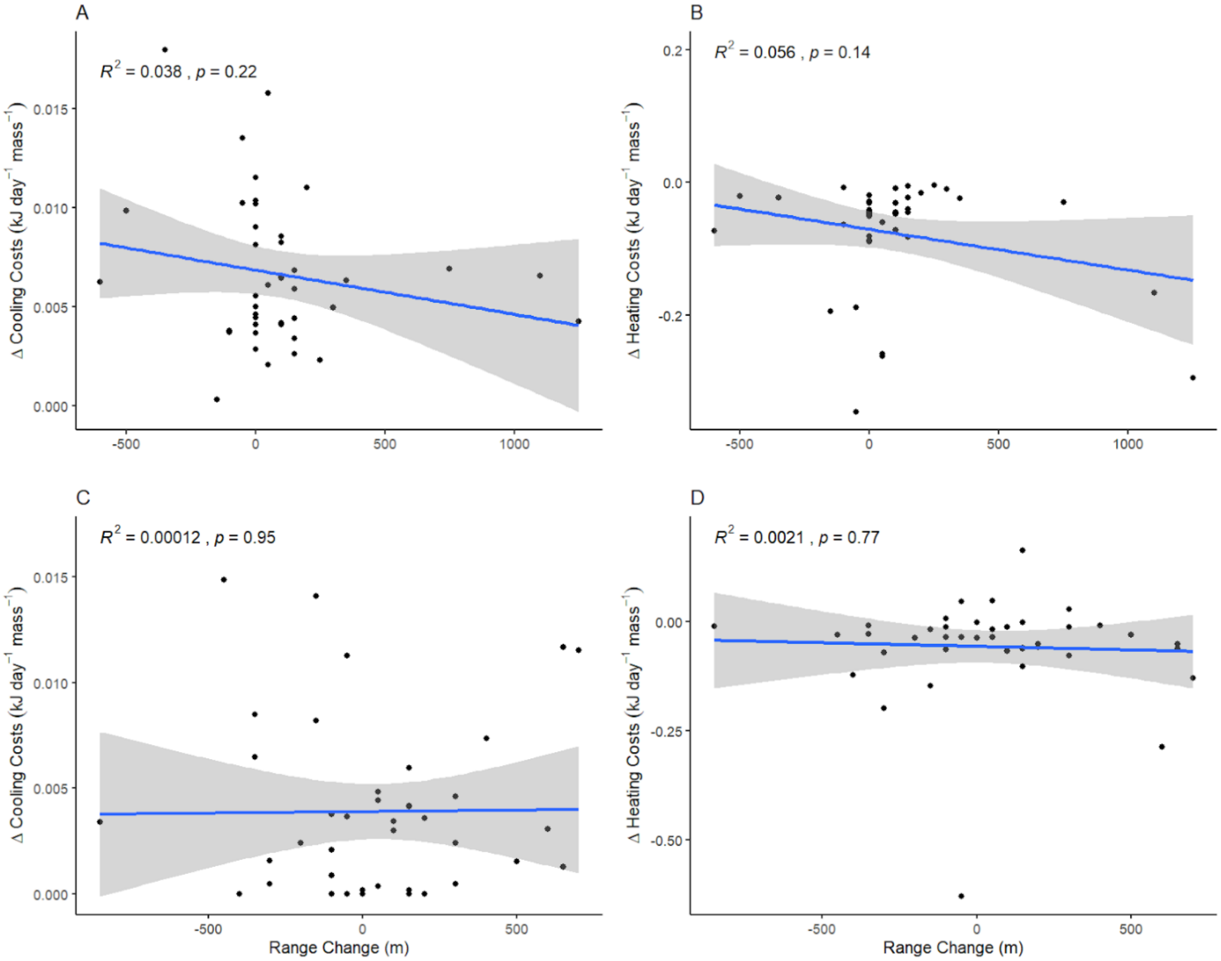


Figure 1: Relationship between mass-specific thermoregulatory costs and observed changes in elevational ranges limits. Thermoregulatory costs at historical elevational limits were calculated under historical and contemporary climate regimes before subtracting historical costs from contemporary costs. Changes in annual cooling costs (A, C) and heating costs (B, D) at the LEL (A, B) and UEL (C, D) are shown for species in both the Front Range and San Juans combined (n = 41).

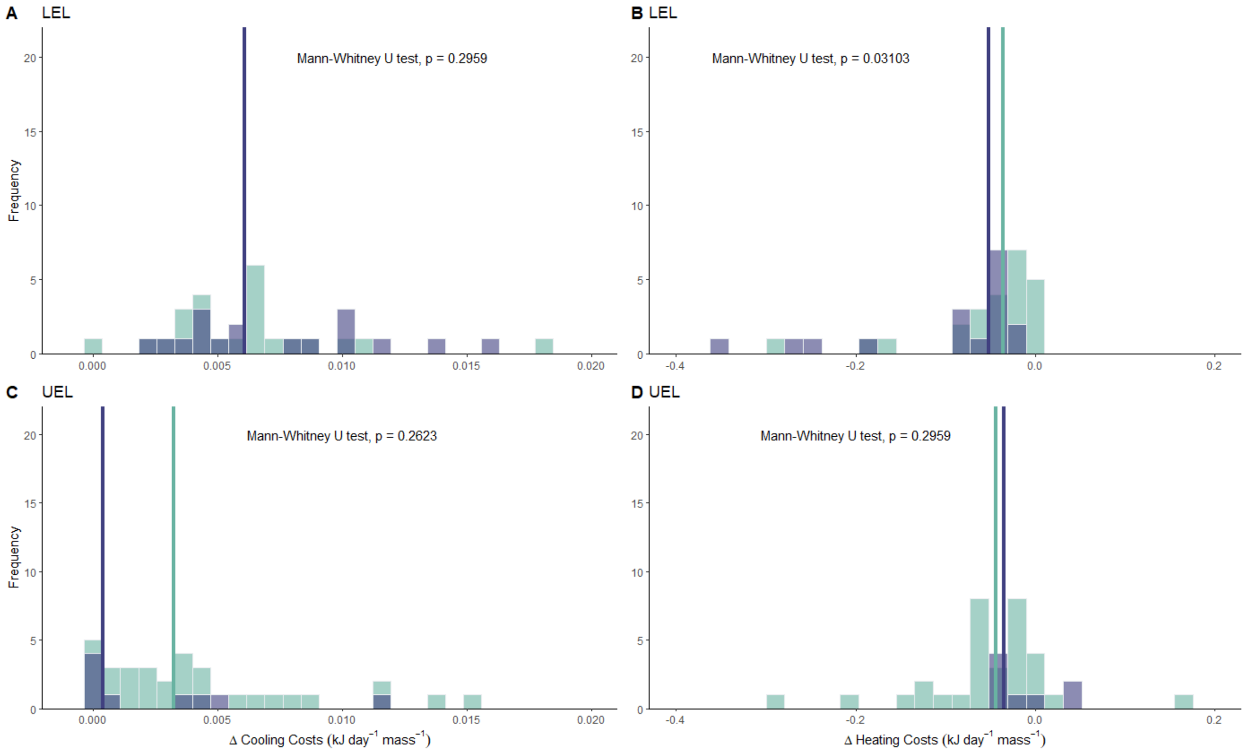


Fig. 2: Change in mass-specific annual cooling and heating costs and movement at elevational range limits. Thermoregulatory costs at historical elevational limits were calculated under historical and contemporary climate regimes for movers (green, LEL movers: n = 24, UEL movers: n = 17) and non-movers (purple, LEL non-movers: n = 32, UEL non-movers: n = 9) before subtracting historical costs from contemporary costs. Species from both mountain ranges are combined (n = 41). Heating costs at the LEL (B) decreased significantly more for non-movers (purple) compared to movers (green) (Mann-Whitney U test; W = 286, p = 0.03103). Vertical lines show group median values.

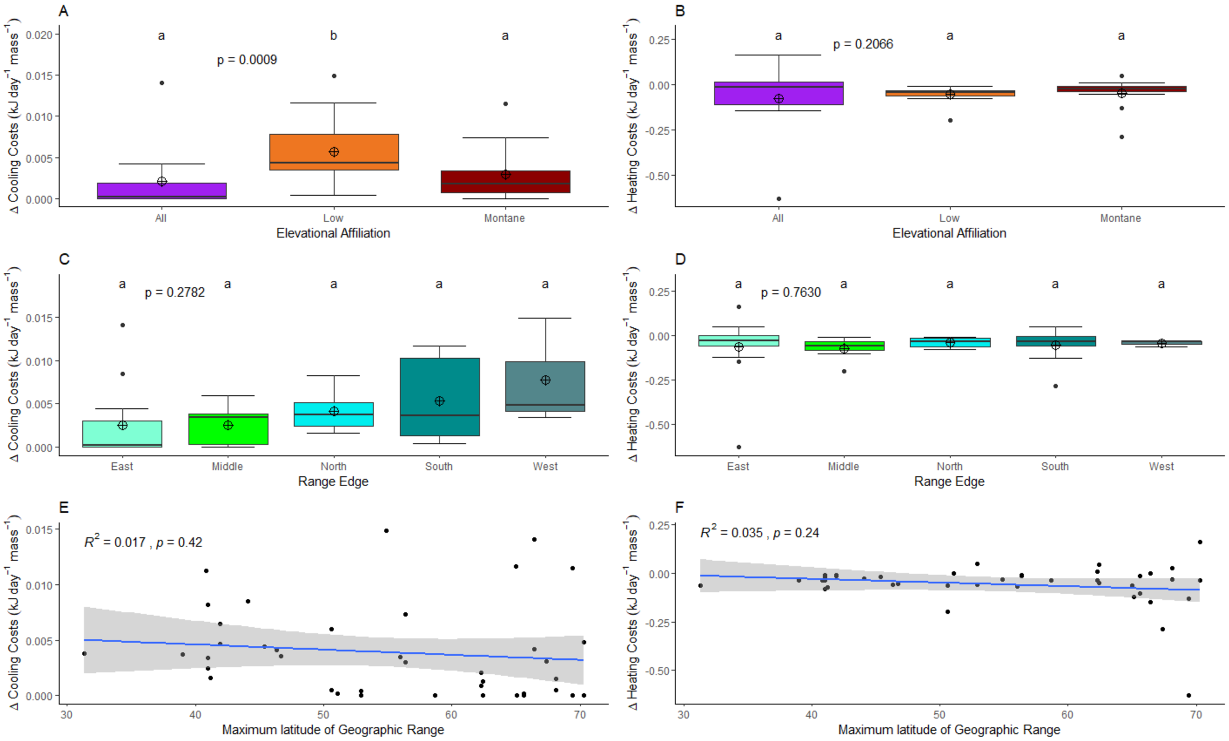


Fig. 3: Changes in annual mass-specific thermoregulatory costs between cold-adapted species and non-cold-adapted species in the Front Range and San Juans combined (n = 41). Here, we define ‘cold-adapted’ as **1)** species affiliated with higher elevations (Armstrong et al. 2011), **2)** species simulated at the southern edge of their species’ geographic ranges, and **3)** species with higher latitudes in their geographic ranges. Cooling (A, C, E) and heating (B, D, F) costs were calculated at the historical UEL in both eras before subtracting historical costs from modern costs. (A) Low species (brown, n = 22) showed a greater increase in cooling costs at the UEL than the Montane (dark red, n = 12) and All (purple, n = 11) groups. (B) No difference in delta heating costs between groups. (C, D) Change in annual thermoregulatory costs at the UEL for species grouped by their simulation location relative to their entire species geographic ranges. No difference between East (teal, n = 13), middle (green, n = 7), North (aquamarine, n = 8), South (blue-green, n = 10), or West (gray, n = 3) groups. Letters above box plots denote statistical similarity or difference between groups. (E, F) Correlation between changes in mass-specific annual thermoregulatory costs and the maximum latitude of species’ geographic ranges for the UEL (n = 41).

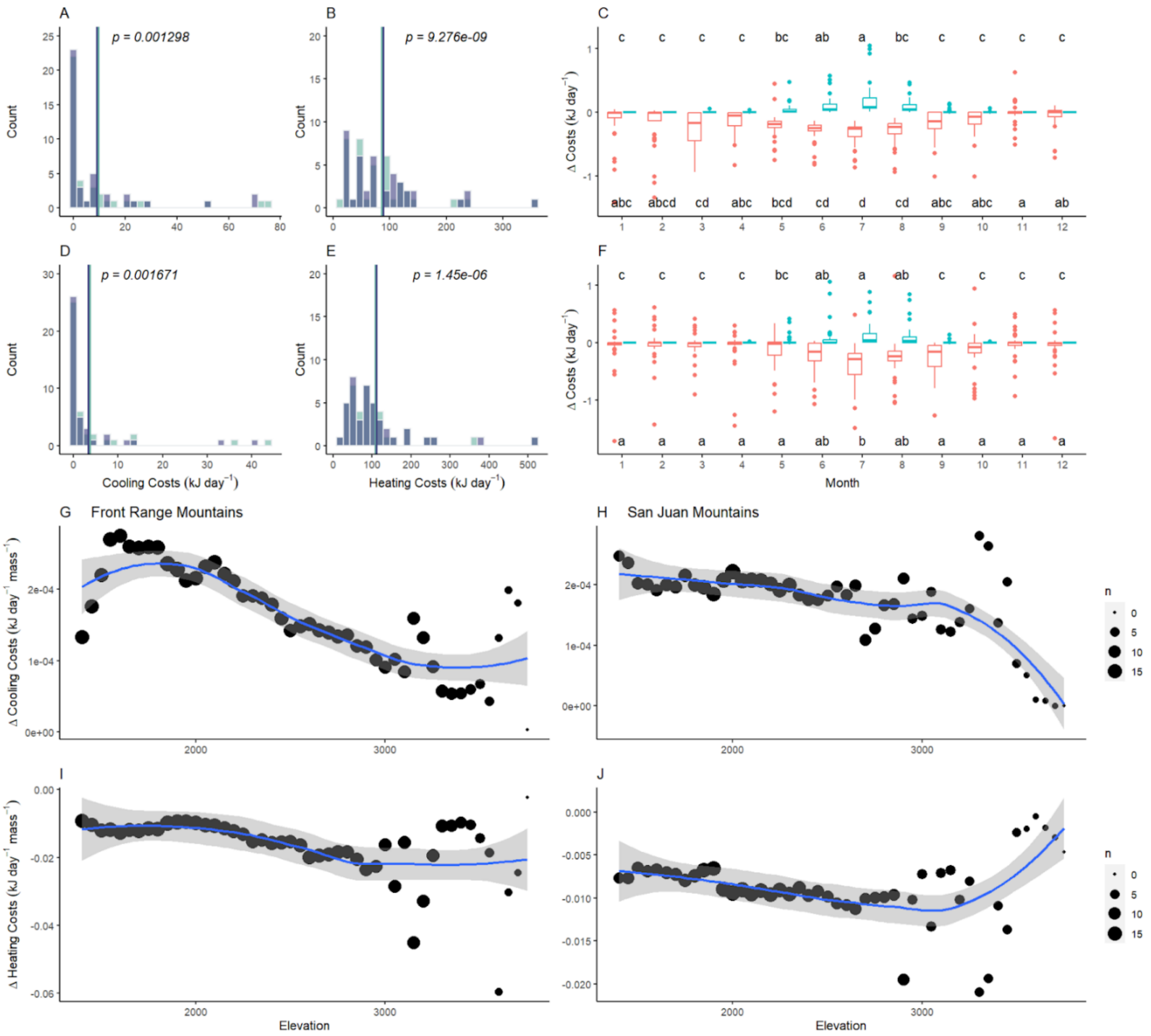


Fig. 4: Community-wide changes in thermoregulatory costs over the past century. (A, B, D, E). Species from both mountain ranges (n = 41) were modeled at their historical range limits under both historical (purple) and contemporary (green) climate regimes. Cooling (A, D) and heating (B, E) costs were summed across all species. Vertical lines show mean values for each era. (C, F) Change in monthly thermoregulatory costs over the past century (contemporary - historical) for small mammal communities. Species were modeled at their historical lower (C) and upper (F) elevational limits under both historical and contemporary climate regimes. Cooling (blue) and heating (red) costs were summed across all species for each month. Letters above box plots denote significant differences.

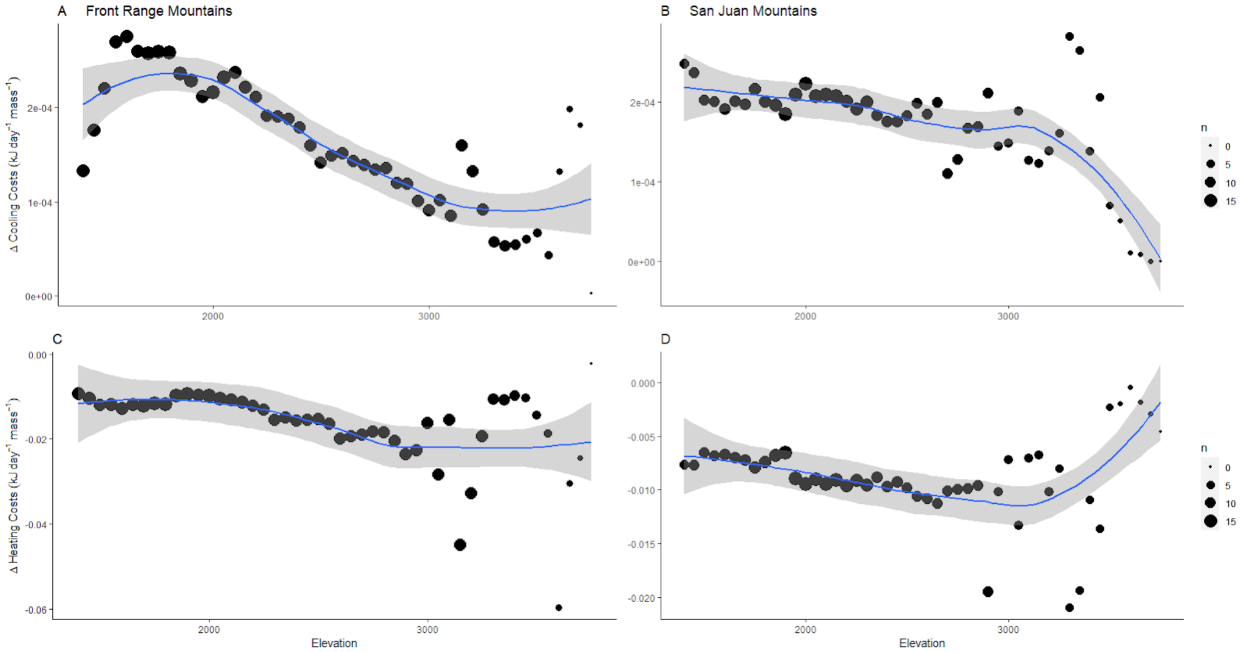


Fig. 5: Mass-specific changes in cooling and heating costs for species in the Front Range (n = 23; A, C) and the San Juans (n = 18; B, D). Species were simulated at all sites between their historical LEL and UEL. Mass-specific changes in cooling (A, B) and heating (C, D) costs were calculated and averaged across all species occurring within each 50 m elevational bin. Point size denotes sample sizes in each bin.

DISCUSSION

Recent studies suggest that increases in thermoregulatory costs over contemporary timescales influence community-level responses to climate change (Riddell et al. 2019; Riddell et al. 2021). At base, vulnerability to climate change is thought to governed by resource imbalances between organisms and their environment (Porter & Gates 1969; Hargreaves et al. 2014), such that physiological aspects of the fundamental niche are often cited as one of the main factors organizing the distribution of species (Williams et al. 2015; Huey et al. 2012; Oswald & Arnold 2012; Gifford & Kozak 2012; Huntley et al. 1989; Cahill et al. 2013). However, few studies explicitly connect range shifts to climate change by quantifying the physiological costs that organisms incur. We endeavored to test whether thermoregulatory costs have changed over time, and directly influence changes in elevational range limits in small mammal communities in the Rocky Mountains. Surprisingly, we found that changes in thermoregulatory costs were not predictive of elevational range shifts in these communities.

Changes in Thermoregulatory Costs Do Not Drive Elevational Range Shifts

We first tested whether changes in annual thermoregulatory costs at historical elevational range limits predicted the direction and magnitude of elevational range shifts for all species in the Front Range and the San Juans combined. We also tested whether cold-adapted species–which shifted upwards the most in our system (McCain et al. 2021)–displayed greater changes in thermoregulatory costs relative to other groups. Contrary to our predictions, our results suggest that changes in thermoregulatory costs are not related to changes in elevational range limits across all species (Fig. 1A, B, C, D). Similarly, we found no evidence to support thermoregulatory costs as drivers of movement patterns annually (Fig. 2) or seasonally (Fig. S1; Table. S1), nor movement in specific directions (Fig. S2, Table. S2). However, greater decreases in heating costs were related to species persistence at historical sites (Fig. 2B, Fig. S1A). Finally, changes in thermoregulatory costs were not greater for cold-adapted species (Fig. 3). None of these results is consistent with changes in thermoregulatory costs being a primary driver of elevational range shifts over the last century.

One possible explanation for this finding is that increases in cooling costs across eras are not large enough to elicit a response. Temperatures in the southern Rocky Mountains have increased by ~ 2.5°C since the beginning of the 20th century (Frankson et al. 2017); mirroring these changes, we found that annual cooling costs at historical range limits have increased for small mammal species (Fig. 4A, D), especially at lower elevations (Fig. 5). To place the magnitude of cooling cost changes into ecological context, we calculated the amount of additional food–either beetles or barley seeds–each species would have to consume per day to offset these increases in cooling costs. We found that the overall increase in daily feeding requirements for evaporative cooling were negligible (Fig. S4-S5). For example, a deer mouse in the Front Range at its LEL would need to eat < 0.001 more beetles each day to meet increases in cooling costs due to climate change. Assuming *Peromyscus maniculatus* eat ~2.5 g of food per day (Vickery et al. 1994), this equates to an increase of 0.1% in daily food consumption. In comparison, Riddell et al. (2019) found that similar-sized birds in the Mojave desert, a community that suffered a major collapse over the past century, needed to increase their beetle intake by > 10 beetles per day to offset increases in cooling costs. This increased food consumption correlated significantly with reductions in occupancy at historical survey sites (Riddell et al. 2019). Our results suggest that meeting the concomitant increases in cooling costs with climate warming is likely trivial for the species in this system.

Changes in Heating Costs Across Space and Time

At the monthly level, we predicted that heating costs would largely increase for small mammals during the fall and spring, reflecting decreases in snow depth and reductions in soil temperatures relative to historical climates (Groffman et al. 2001). We also predicted that increases in heating costs would peak at mid-elevation sites (~ 3000 m; Steger et al. 2013; Vaughan et al. 2013; Roberts et al. 2021). We expected that elevational range shifts would correlate with the magnitude of heating cost increases at these elevations and during these seasons.

While annual cooling costs increased, heating costs largely decreased over the past century in our system, and these decreases were roughly four-fold higher than the increases in cooling costs (Fig. 4B, E). Annually, mid elevation sites (~3000 m) showed the largest decreases in average heating costs across our species and in both mountain ranges (Fig. 5C, D). At the monthly scale, though, the highest number of species displaying increases in heating costs appeared during the months of April at the LEL (36.6%; Table S3) and November at the UEL (36.6%; Table S3). The average elevational range limits for those species experiencing increases in heating costs generally occurred within the band predicted to be most stressful (LEL: 1582.5, SD = 324.56; UEL: 3105.667, SD = 583.3605). However, monthly changes in heating costs did not predict elevational range shifts (Table S1-S2). Finally, species occupying mid-to-high elevation sites experienced decreases in heating costs (Fig. 5C, D), and were not more likely to shift their elevational ranges (Fig. S3).

Our results do not support the hypothesis that increases in heating costs drive elevational range shifts in a seasonally or elevation-specific manner. Rather, we provide evidence that increases in air temperature can increase or decrease heating costs depending on the species and the location of their elevational limits (Table S3). Kearney (2020) similarly showed that heating costs for simulated hibernating mammals largely decreased under contemporary warming, though a subset of sites in the Southern Rocky mountains displayed increases in costs due to reductions in snow depth. Likewise, we found that some species displayed increases in heating costs at their elevational limits, particularly during April and November, and these species occurred mainly at low-to-mid elevations (~1500 to 3100 m). This lends some support to past studies in that species within this elevational band and temporal scope appear to be particularly vulnerable to increases in heating costs (Roberts et al. 2021; Slatyer et al. 2021); however, in all months, the number of species showing no change or decreases in heating costs was always higher (Table S3).

While we were not able to connect changes in heating costs and elevational shifts to snow depth directly, our approach to modeling winter soil temperatures–which has also been validated in situ by other studies (Kearney et al. 2020; Fitzpatrick et al. 2019)–estimates changes in microclimate temperatures that are likely experienced by small mammals in our study system (Fig. S7). We cannot rule out, however, the impact that acute, severe weather events might have on the connection between changes in heating costs and elevational range shifts. By using 30-year average climate data in the model input, our approach masks potentially important weather extremes. For instance, Roberts and colleagues (2021) showed that years with less snowfall increase cold exposure and lethal levels of energy depletion for montane beetles, potentially driving local extirpation at specific elevations. Finer-scale approaches focusing on interannual variation in climate variables may have more power to detect elevational range shifts via extreme changes in thermoregulatory costs or threshold effects due to factors such as cold snaps (Kearney et al. 2020; Garrett et al. 2022; Fitzpatrick et al. 2019).

A Potential Role for Phenological Shifts

One potential caveat for our heating costs results is that we assumed constant phenological traits across species and elevations, such that the emergence date for hibernators remained unchanged between the two time periods and across elevations. In reality, emergence dates are shifting earlier under climate warming in some of our species. Inouye et al. (2000) showed that yellow-bellied marmots (*Marmota flaviventris*) have shifted their emergence date ~38 days earlier since 1984 at the Rocky Mountain Biological Laboratory (RMBL) in the Colorado Front Range. Snow depth is increasing at RMBL, despite stability in the date of snowmelt, and marmots are emerging earlier in the season likely due to air temperature cues (Inouye et al. 2000). To determine how phenological shifts affect estimates of heating costs, we simulated two scenarios using marmots as an example: one scenario where phenologies remained constant between historical and contemporary periods, and another where contemporary emergence dates shifted earlier by 1 month. By changing hibernation emergence dates, our simulations revealed that instead of decreasing heating costs, marmots experienced a 20.88% and 16.08% increase in daily heating costs at the LEL and UEL respectively (Table S4). This confirms what Inouye and colleagues (2000) predicted: that earlier emergence places greater energetic stress on marmots in the Colorado Rockies via increases in heating costs. Our results also provide support to the prediction that cold exposure may be impacted most strongly by changes in spring phenology (Fitzpatrick et al. 2019; Kelsey et al. 2021).

How such changes in phenology relate to our range shift analyses is difficult to say. If most hibernators are shifting their emergence phenology, we may have generally underpredicted increases in heating costs for hibernators in our analysis, but emergence cues vary across species (Findaley-Robinson et al. 2023). For example, yellow-bellied marmots respond to changes in air temperature despite no change in snowmelt date (Inouye et al. 2000); yet, Columbian ground squirrels (*Urocitellus columbianus*) have progressively delayed their emergence as snowmelt dates became later, despite slight increases in temperature (Lane et al. 2012). A recent study on edible dormice (*Glis glis)* further showed that the strength of the relationship between emergence date and temperature depended strongly on food availability in the previous summer (Fietz et al. 2020). Robust data on recent phenological changes in hibernation emergence across species are lacking (Wells et al. 2020) and we cannot reliably predict how heating costs might change in our analysis as a result. Phenological shifts notwithstanding, changes in heating costs showed no relationship to movement at elevational limits for all species combined (Fig. 1B, E), even when hibernators were removed. Nevertheless, incorporating the effects of phenological mismatch could yield new insights on changes in heating costs as they relate to elevational range shifts.

Small Mammals Appear Buffered from Increases in Thermoregulatory Stress

Our results suggest that small montane mammals are relatively buffered from increases in cooling costs despite widespread warming in the southern Rockies (Frankson et al. 2017; Mathewson et al. 2016). Smaller animals can have higher mass-specific environmental heat loads owing to their higher surface-area-to-volume ratios (Fuller et al. 2016); however, small mammals also have a greater capacity to seek out cooler microclimates for thermoregulation (Schmidt-nielsen 1965; Riddell et al. 2021). Fossoriality is common among our species, such that small mammals are shielded from extreme temperature fluctuations via the buffering effects of soil (White 2003; Nikol'skii & Savchenko 2002). Many small mammal species are also nocturnal and thus not exposed to peak daily temperatures during the hottest parts of the year (Walsburg 2000). Across small mammals, physiological adaptations to xeric environments also minimize the need for free-standing water (Nagy 1994). While not all of our species are xeric specialists, changes in cooling costs across eras were small, and likely represent negligible increases in daily water requirements (Fig. S4-S5).

The buffering effects of snow during mid-winter generally keep soil surface temperatures near zero (Pauli et al. 2013; Roberts et al. 2021; Fig. S6) and changes in thermoregulatory costs appear to be minimized during colder months (Fig. 4C, D) when most high-altitude mammals are either hibernating or utilizing daily torpor underground. Heating costs largely decreased across our species (Fig. 4-5), especially during the summer (Fig. 4C, F). Still, heating costs increased for a subset of species during specific months (Table S3), and phenological shifts could drastically increase heating costs for some hibernators (Table S4; Kearney 2020). Nevertheless, changes in thermoregulatory costs were not associated with observed range shifts across species (Fig. 1-3). Overall, the findings in our study suggest the majority of range shift responses in our system stem from other abiotic or biotic pressures, rather than changes in thermoregulatory costs alone.

The Role of Biotic Interactions in Mediating Elevational Range Shifts

Notably, our approach ignores important aspects of community ecology in an attempt to identify the biophysical signals of elevational range shifts. Indeed, the factors governing the elevational distributions of organisms are multifaceted and complex (Sexton et al. 2009), and we recognize that elevational distributions are not governed by thermoregulatory costs alone (Slatyer & Schoville 2016). Ecological factors play an integral part in the distribution of species across the landscape. Broadly, negative correlations between abundances of potential competitors, or between predators and prey, suggest that biotic interactions play an outsized role in structuring species distributions (Bullock et al. 2000; deRivera et al. 2005). Moreover, changes in edaphic conditions (Brown & Vellend 2014; Frei et al. 2010), food availability (Preuss & Padial 2021), and habitat continuity (Beever et al. 2003) are all also known to mediate elevational range shifts.

Plant cover plays an important role in modulating the microclimates and biotic communities that organisms experience (Martin & Murray 2011; Garcia & Clusella-Trullas 2019; Suggitt et al. 2010). Quantifying variation in the extent of plant cover over the past century was beyond the purview of this study. However, Moritz et al. (2008), in a similar study analyzing elevational range changes in Yosemite National Park mammal communities, showed that high-altitude habitat was largely similar in 2003 compared to 1914, and ecological traits were poor predictors of upward range shifts. Habitat change via anthropogenic land use seems to have partially driven upslope migration in low-elevation species in the Front Range, but not in the San Juans (McCain et al. 2021). Limiting our analysis to only species in the San Juans, however, did not improve the predictive power of our analyses. Also, land-use change cannot explain upward shifts at middle to high elevations, where most species' historical range limits occurred (McCain et al. 2021; Fig. S2).

Limitations

Admittedly, our results should be interpreted with some caution. For one, we did not control for potential phylogenetic effects. However, we argue that this is unlikely to undermine our central results. We chose to present non-phylogenetically-corrected values for several reasons: 1) McCain et al. (2021) showed that observed range shift responses in our species showed negligible phylogenetic signal, and they similarly presented non-corrected values for their analyses of range shifts 2) all but one of the traits in our analyses showed no significant phylogenetic signal (Table 2), and 3) our analyses generally produced negative results. While changes in mass-specific heating costs at the LEL did exhibit significant phylogenetic effects, they do not explain observed range shifts, and thus, using corrected values would probably further decrease the likelihood of detecting significant relationships between the response and predictor variables (Felsenstein 1985). Also, changes in mass-specific heating costs were minimized at lower elevations in our system (Fig. 5), and maximized during the summer months (Fig. 4C, F), when heating costs were least likely to increase and drive species range shifts. Finally, movement at the LEL showed some relationship to changes in anthropogenic land use in the Front Range, obscuring our confidence in thermoregulatory costs being the sole driver of elevational range shifts at the LEL compared to the UEL (McCain et al. 2021). Nevertheless, we acknowledge that a failure to correct for phylogenetic effects may have influenced the magnitude of cost changes and potentially the results for a subset of our analyses.

We were also necessarily limited in the extent and number of variables we could realistically include in this analysis. For example, we did not include variation in population-level traits to test for the potential buffering effects of phenotypic plasticity and evolution over our focal time period. Plasticity and evolution in morphological and physiological traits are known to influence organismal responses to climate change over short timescales (Grant & Grant 1989; Boyles et al. 2011), and both can be incorporated in mechanistic models, though examples in the literature are rare (Nicotra et al. 2010). Interspecific differences in trait variation could have biased our results if evolutionary potential, or the degree of plasticity in relevant traits, varied among our focal species (Kearney et al. 2016; Buckley 2008). For example, our estimates of thermoregulatory costs could have changed less than we predicted due to plasticity or evolution in traits relevant to heat flux. However, Enriques-Urzelai et al. (2020) showed that mechanistic modeling frameworks incorporating phenotypic variation in biophysical traits offered limited protection in buffering organisms from exposure to climate change along elevational gradients. We elected instead to keep species traits constant over the past ~100 years of climate warming, following other similar resurvey studies (Riddell et al. 2021; Riddell et al. 2019; Moritz et al. 2008; Rowe et al. 2015; McCain & King 2014). Our approach incorporates behavioral avoidance of changing temperatures via microhabitat buffering, which is predicted to have a greater effect on exposure to climate change compared to variation in physiological traits (Enriques-Urzelai et al. 2020; Riddell et al. 2021).

Modeling microclimates in physiographically diverse habitats requires fine-grained forcing data, and our approach may be vulnerable to discrepancies between observed and predicted values. Climate changes rapidly across mountain ranges due to the adiabatic lapse rate, differences in radiative intensity, humidity, cold-air drainage, and snowpack among other factors (Daly et al. 2000; Geiger et al. 1995). We elected to use the PRISM dataset for its high-spatial resolution and accuracy in incorporating montane-specific meteorological phenomena. Coupled with the microclimate model from NicheMapR, we included the effects of snowpack in driving operative temperatures for the species in our study. While our approach showed a high degree of correlation between observed and predicted soil temperatures in snowy months (Fig. S7), and demonstrates the buffering effect of snow on soil temperatures (Fig. S6), our estimates of snow depth across elevation proved unreliable. Snow depth varies as a function of elevation, but also wind speed, humidity, slope, aspect, and vegetation structure (Barlage et al. 2010; Ford et al. 2013). Scouring by wind plays a crucial role in determining snow depth and cover in the mountains and can cause significant variation in these variables over physiographically-heterogenous sites (Purves et al. 2017). New methods for measuring snowpack are emerging (LIDAR, etc.) and could drastically improve our understanding of how snow depth and snow cover vary along each of these axes (Kinar & Pomeroy 2015). Looking forward, similar studies will benefit greatly from finer-grained approaches to modeling thermoregulation in montane mammals as a function of spatial variation in snowpack.

Summary

To our knowledge, our study is the first to apply biophysical simulations of heat flux to examine the abiotic drivers of elevational range shifts. We also applied novel methods to understand the impact of snow on microclimate temperatures for high-elevation mammal communities (Kearney et al. 2020). Observed shifts in elevational ranges showed no relationship to changes in thermoregulatory costs at historical range limits at the community scale. We demonstrated that cooling costs are increasing under climate warming, but these changes are small, and small mammal communities in Colorado are most likely buffered from the negative effects of climate change on thermoregulation. Our findings further suggest that changes in thermoregulatory costs are not distributed equally across all elevations and months of the year. Cooling costs increase the most at low elevations during the summer, when small montane mammals are generally active and non-torpid. Heating costs also decreased the most during the summer, but including changes in winter phenology into mechanistic models of heat flux could uncover divergent patterns, once more robust data become available (Wells et al. 2022). For mammals living in mountainous environments, we suggest that more emphasis should be placed on biotic interactions as potential drivers of range shifts under climate change, following past studies (Slatyer & Schoville et al. 2016; Hargreaves et al. 2014). Overall, our results lend support to the findings of past studies: that small mammal communities tend to be more buffered from exposure to climate change than other taxa (Riddell et al. 2021), and the mechanistic drivers of range shifts continue to be elusive (Beissenger & Riddell 2021).

SUPPLEMENTARY MATERIALS

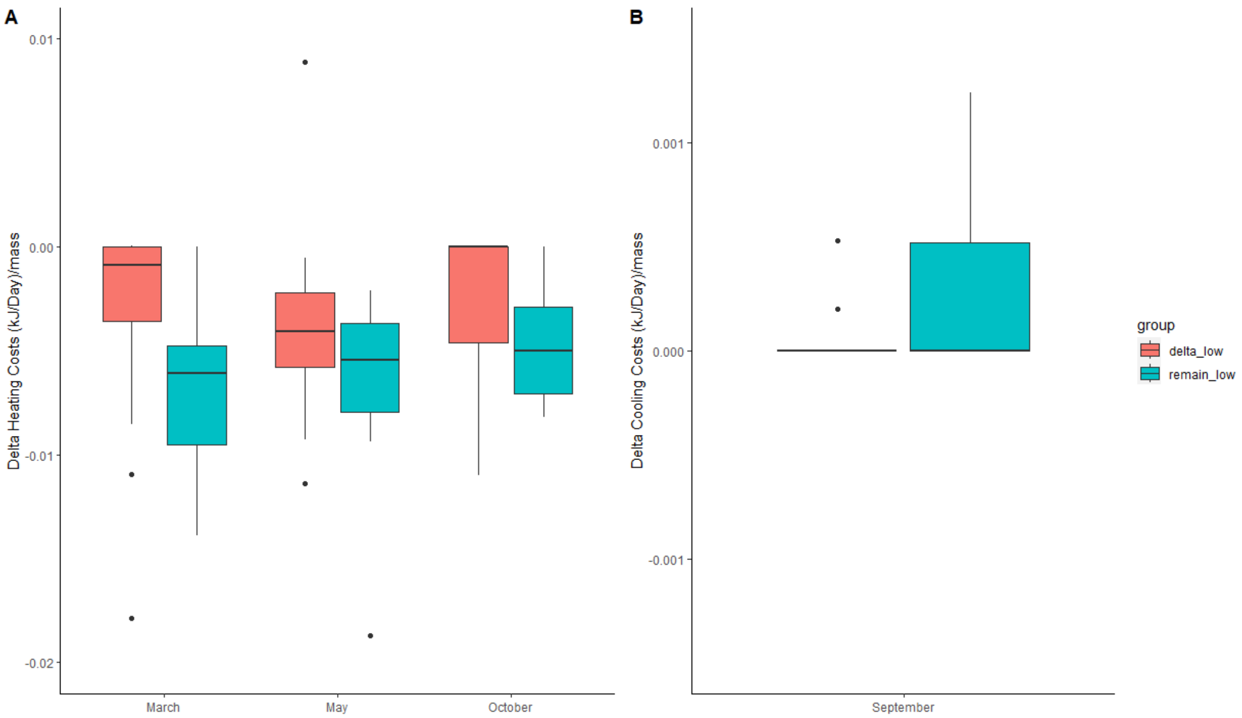
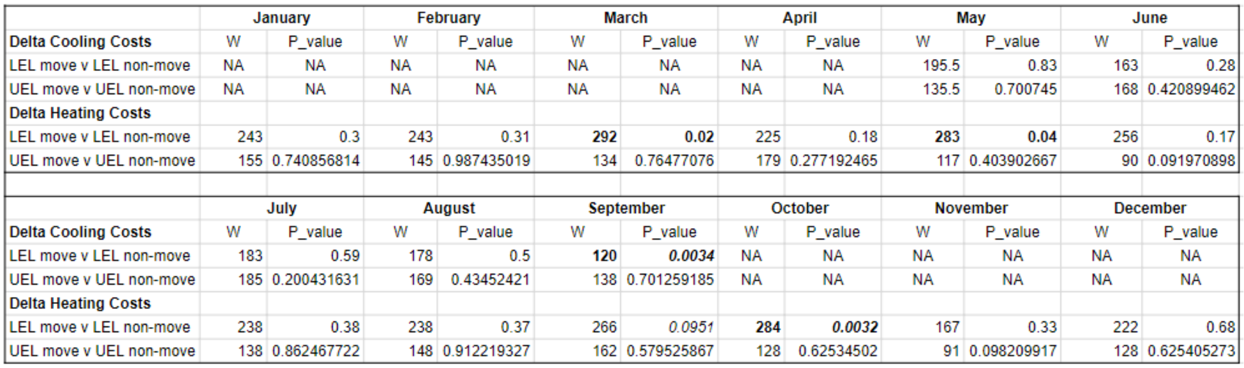


Fig. S1: Significant results from monthly analysis of mass-specific delta thermoregulatory costs at the LEL in movers (delta_low, red) versus non-movers (remain_low, blue) for both mountain ranges combined. In each comparison, the group with the greatest change in thermoregulatory costs was the group that did not shift its elevational limit. A) Delta heating costs at the LEL for the months of March, May, and October; B) delta cooling costs at the LEL for the month of September.

Table S1: Results from analysis of change in monthly cooling and heating costs for movers and non-movers in both mountain ranges combined. Significant results are highlighted in bold. For all significant comparisons, the group that did not shift its elevational range limit was the group displaying the greater magnitude of thermoregulatory cost change. Costs were converted to mass-specific kJ/Day. Sample sizes for comparisons: **1)** LEL move = 24, LEL non-move = 17, **2)** UEL move = 32, UEL non-move = 9.



	January		February		March		April		May		June	
Delta Cooling Costs	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value
LEL move v LEL non-move	NA	NA	NA	NA	NA	NA	NA	NA	195.5	0.83	163	0.28
UEL move v UEL non-move	NA	NA	NA	NA	NA	NA	NA	NA	135.5	0.700745	168	0.420899462
Delta Heating Costs												
LEL move v LEL non-move	243	0.3	243	0.31	**292**	**0.02**	225	0.18	**283**	**0.04**	256	0.17
UEL move v UEL non-move	155	0.740856814	145	0.987435019	134	0.76477076	179	0.277192465	117	0.403902667	90	0.091970898

	July		August		September		October		November		December	
Delta Cooling Costs	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value
LEL move v LEL non-move	183	0.59	178	0.5	**120**	***0.0034***	NA	NA	NA	NA	NA	NA
UEL move v UEL non-move	185	0.200431631	169	0.43452421	138	0.701259185	NA	NA	NA	NA	NA	NA
Delta Heating Costs												
LEL move v LEL non-move	238	0.38	238	0.37	266	*0.0951*	**284**	***0.0032***	167	0.33	222	0.68
UEL move v UEL non-move	138	0.862467722	148	0.912219327	162	0.579525867	128	0.62534502	91	0.098209917	128	0.625405273

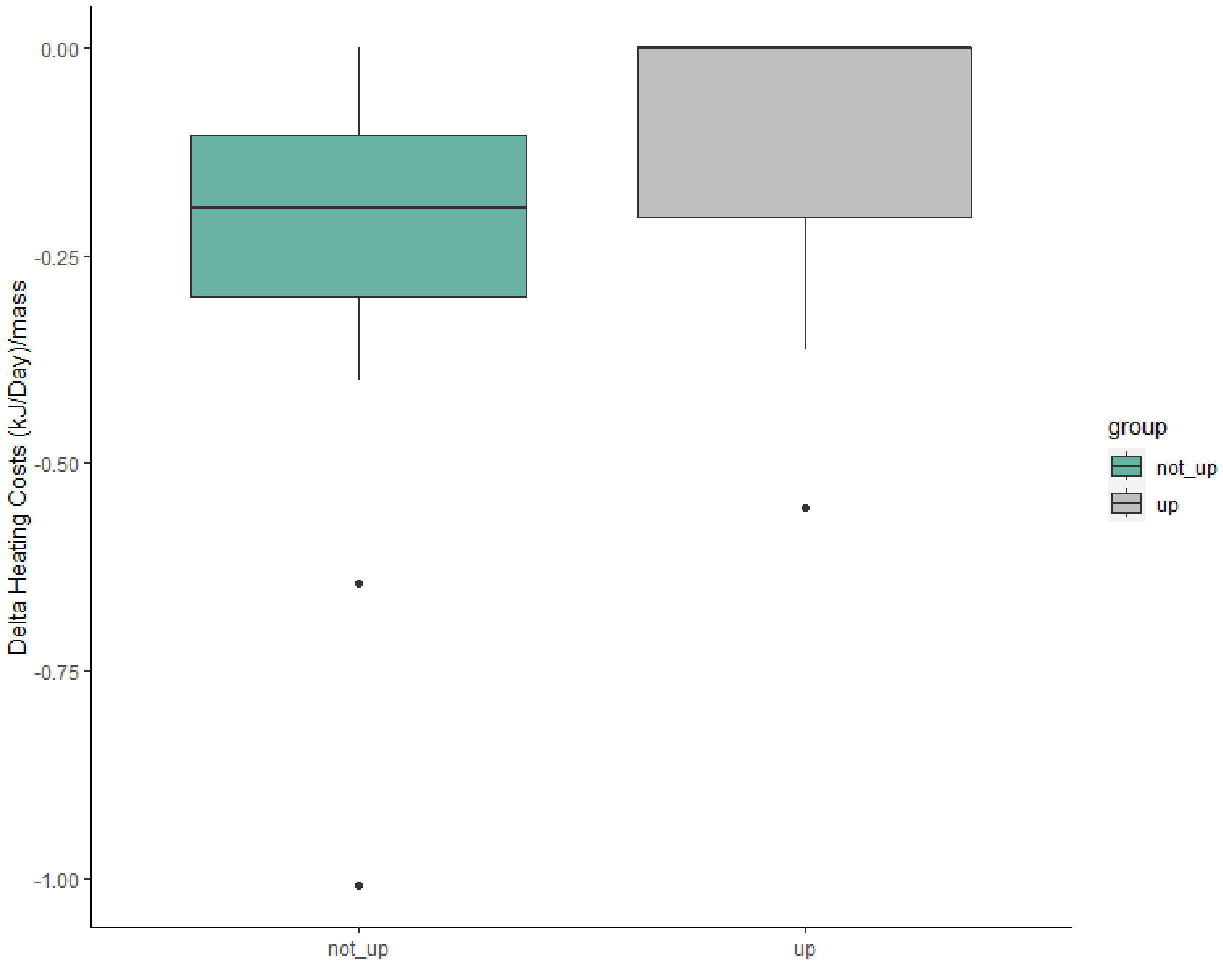
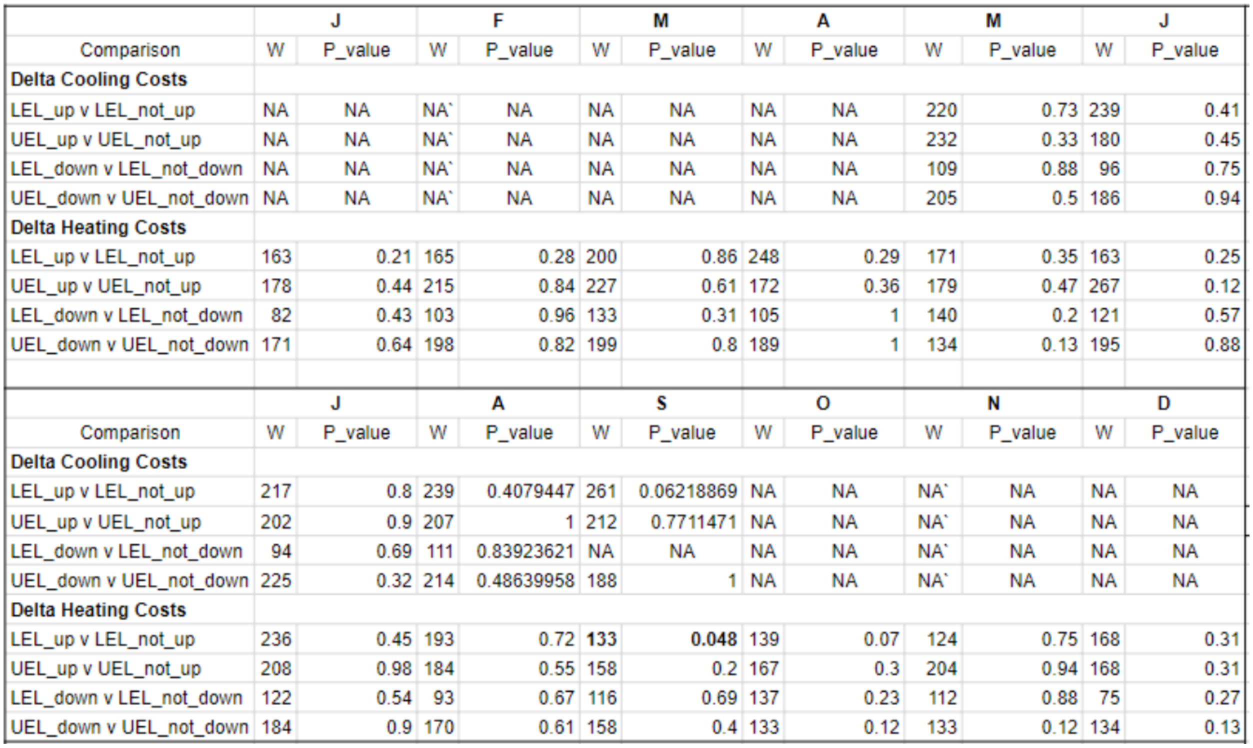


Fig. S2: Significant results from monthly analysis for mass-specific delta heating costs at the LEL in the month of September for species in both mountain ranges (n = 41). Species that shifted their LEL upwards (blue) were compared to all other species responses (red).

Table S2: Results from analysis of change in monthly cooling and heating costs for directional movement. Significant results are highlighted in bold. For significant comparisons (October heating costs, LEL_up v LEL_not_up), LEL_not_up displayed the greater magnitude of thermoregulatory cost change. Costs were converted to mass-specific kJ/Day. Sample sizes for comparisons: **1)** LEL_Up = 18, LEL Not Up = 23, **2)** LEL down = 9, LEL not down = 32, **3)** UEL up = 19, UEL not up = 22, **4)** UEL down = 15, UEL not down = 26.



	J		**F**		**M**		**A**		**M**		**J**	
Comparison	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value
Delta Cooling Costs												
LEL_up v LEL_not_up	NA	NA	NA`	NA	NA	NA	NA	NA	220	0.73	239	0.41
UEL_up v UEL_not_up	NA	NA	NA`	NA	NA	NA	NA	NA	232	0.33	180	0.45
LEL_down v LEL_not_down	NA	NA	NA`	NA	NA	NA	NA	NA	109	0.88	96	0.75
UEL_down v UEL_not_down	NA	NA	NA`	NA	NA	NA	NA	NA	205	0.5	186	0.94
Delta Heating Costs												
LEL_up v LEL_not_up	163	0.21	165	0.28	200	0.86	248	0.29	171	0.35	163	0.25
UEL_up v UEL_not_up	178	0.44	215	0.84	227	0.61	172	0.36	179	0.47	267	0.12
LEL_down v LEL_not_down	82	0.43	103	0.96	133	0.31	105	1	140	0.2	121	0.57
UEL_down v UEL_not_down	171	0.64	198	0.82	199	0.8	189	1	134	0.13	195	0.88

	J		**A**		**S**		**O**		**N**		**D**	
Comparison	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value	W	P_value
Delta Cooling Costs												
LEL_up v LEL_not_up	217	0.8	239	0.4079447	261	0.06218869	NA	NA	NA`	NA	NA	NA
UEL_up v UEL_not_up	202	0.9	207	1	212	0.7711471	NA	NA	NA`	NA	NA	NA
LEL_down v LEL_not_down	94	0.69	111	0.83923621	NA	NA	NA	NA	NA`	NA	NA	NA
UEL_down v UEL_not_down	225	0.32	214	0.48639958	188	1	NA	NA	NA`	NA	NA	NA
Delta Heating Costs												
LEL_up v LEL_not_up	236	0.45	193	0.72	**133**	**0.048**	139	0.07	124	0.75	168	0.31
UEL_up v UEL_not_up	208	0.98	184	0.55	158	0.2	167	0.3	204	0.94	168	0.31
LEL_down v LEL_not_down	122	0.54	93	0.67	116	0.69	137	0.23	112	0.88	75	0.27
UEL_down v UEL_not_down	184	0.9	170	0.61	158	0.4	133	0.12	133	0.12	134	0.13

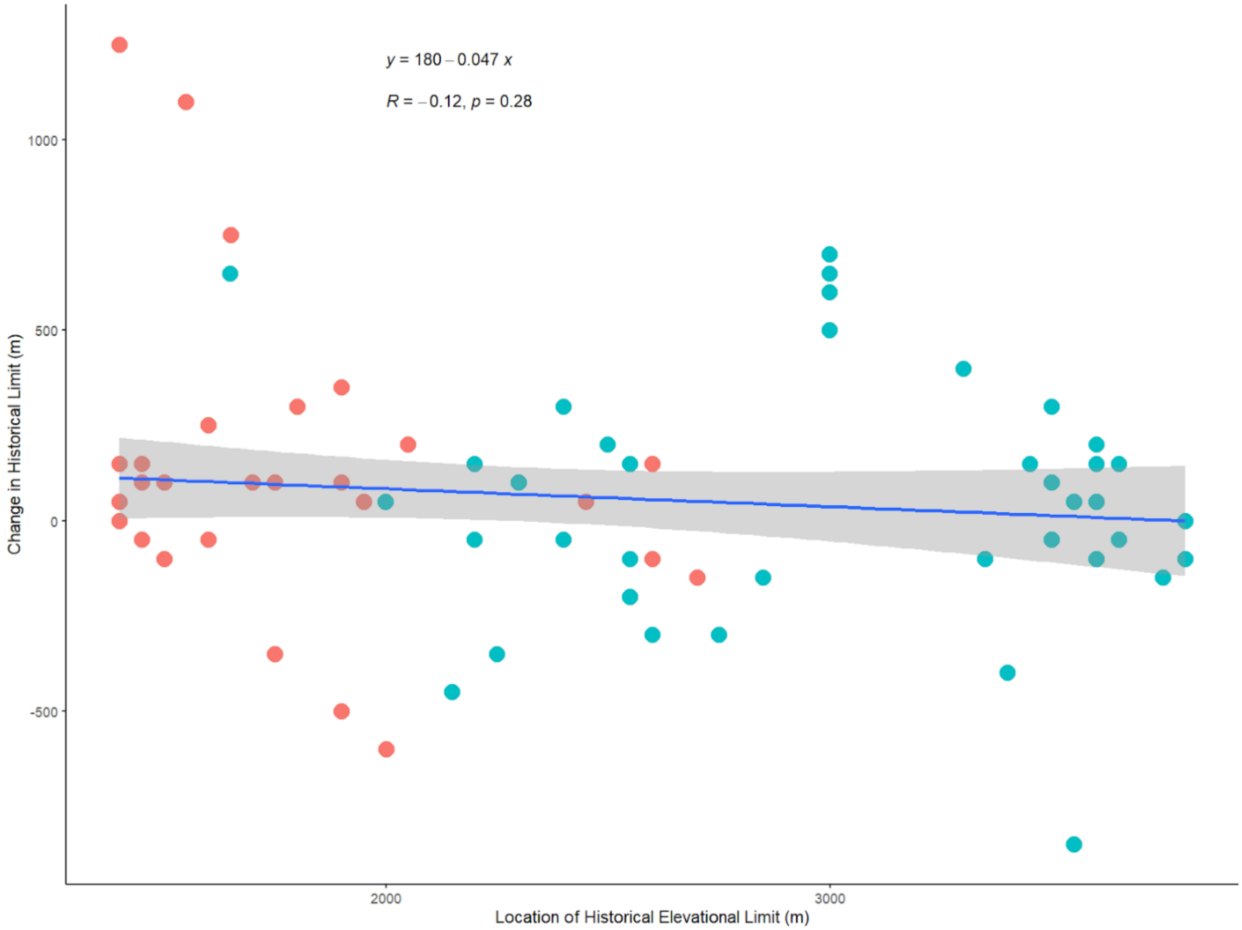


Fig. S3: Elevational change at range limits as a function of altitude. Shifts in species' range limits were uniform across elevational bins (p = 0.28). UEL's (blue) and LEL's (red) are shown for species from both the Front Range and San Juans (n = 41). Blue line is the linear regression with 95% confidence intervals in gray.

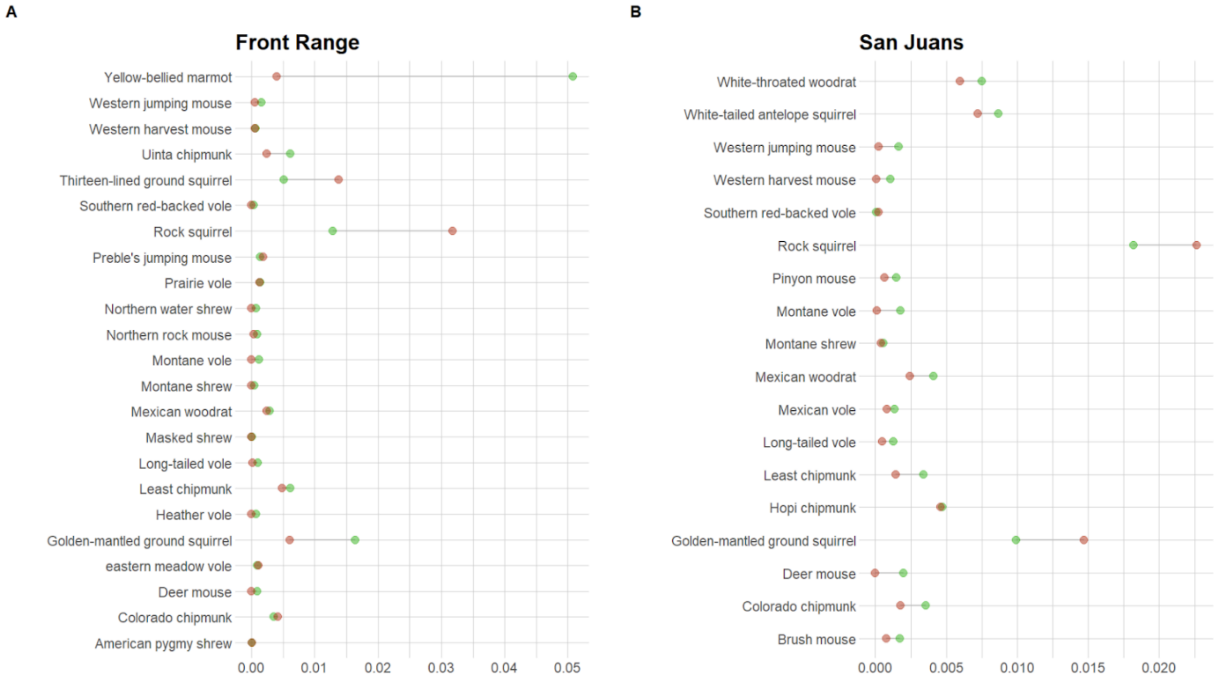


Fig. S4: The number of additional insects per day required to offset the increase in cooling costs assuming a diet of Darkling beetles (*Edrotes ventricosus*). Annual delta cooling costs were calculated at the historical LEL (red dots) and UEL (green dots) for mammal species in the Front Range and the San Juans combined. Beetle numbers (x-axis) are absolute and not mass corrected. Calculations follow those made in Riddell et al. (2019).

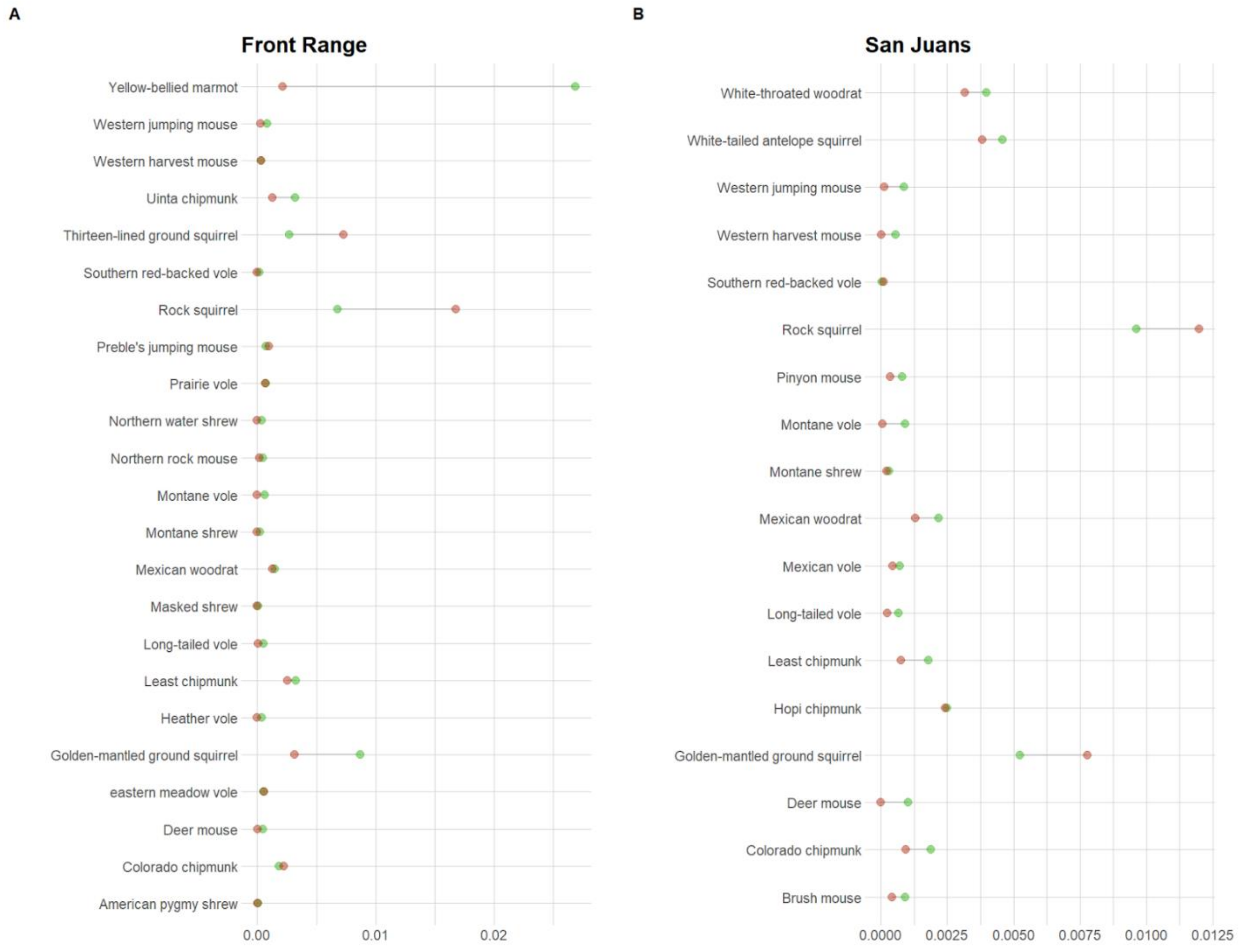
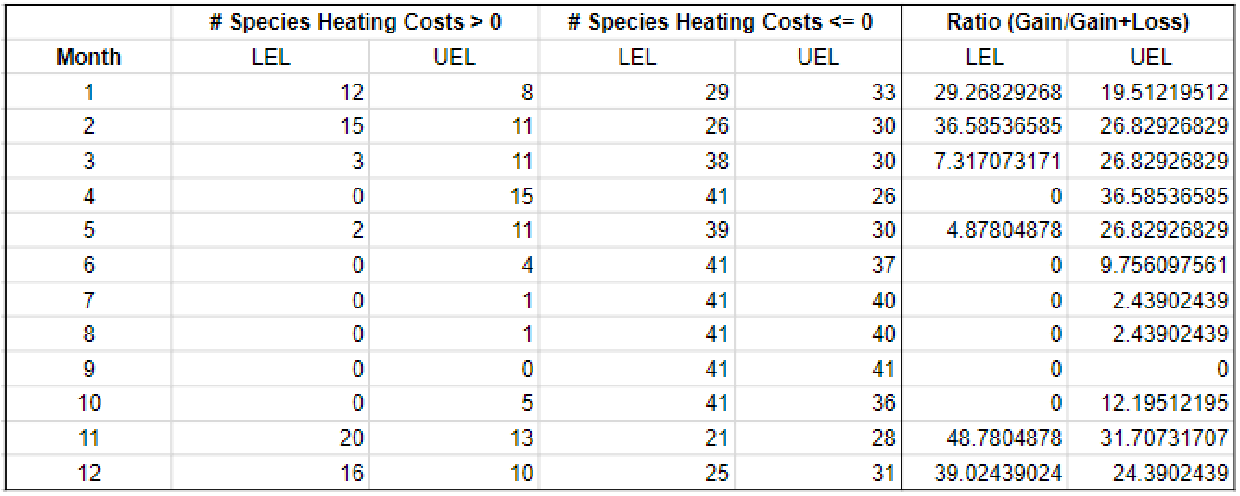


Fig. S5: The number of additional grams of seeds per day required to offset the increase in cooling costs over the past century, assuming a diet of husked barley seeds (*Hordeum vulgare*; Frank 1988). Annual delta cooling costs were calculated at the historical LEL (red dots) and UEL (green dots) for mammal species in the Front Range and the San Juans. Seed mass (x-axis) is absolute and not corrected for species' mass.

Table S3: Ratio of species showing increases in heating costs relative to decreasing or unchanging heating costs in each month for both elevational limits. Qualitatively, more species show increases in heating costs at the LEL in early winter and late fall, and spring and fall at the UEL.



	# Species Heating Costs > 0		# Species Heating Costs <= 0		Ratio (Gain/Gain+Loss)	
Month	LEL	UEL	LEL	UEL	LEL	UEL
1	12	8	29	33	29.26829268	19.51219512
2	15	11	26	30	36.58536585	26.82926829
3	3	11	38	30	7.317073171	26.82926829
4	0	15	41	26	0	36.58536585
5	2	11	39	30	4.87804878	26.82926829
6	0	4	41	37	0	9.756097561
7	0	1	41	40	0	2.43902439
8	0	1	41	40	0	2.43902439
9	0	0	41	41	0	0
10	0	5	41	36	0	12.19512195
11	20	13	21	28	48.7804878	31.70731707
12	16	10	25	31	39.02439024	24.3902439

Table S4: Effect of changes in emergence date on daily heating costs. Delta annual heating costs for *Marmota flaviventris* were calculated at the historical LEL and UEL under two phenological scenarios: the first where marmots emerge from hibernation at the beginning of May in both modern and historic climate scenarios, and another where marmots emerge at the beginning of April in the modern period only (Inouye et al. 2008). Change expressed in delta kJ/Day and as the percent change relative to historical daily heating costs.

Limit	**September - May**	**September - April**
LEL	-11.467833 (-5%)	47.22258 (+20.88%)
UEL	-3.839917 (-0.74%)	83.77650 (+16.08%)

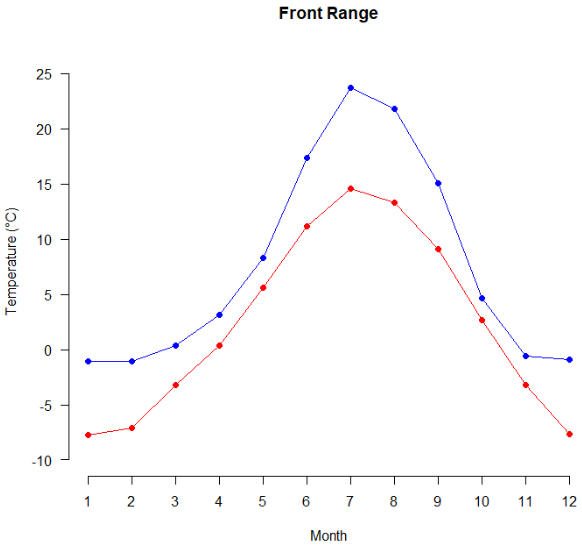


Fig. S6: Monthly mean air temperature (red) and simulated soil surface temperature (blue) across all simulation sites (1400 - 3750 m; n = 48) for each month of the year in the Front Range and San Juan mountains. Soil temperatures are uncoupled from air temperatures in winter months due to the insulative effects of deep snow. Soil temperature data were generated from NicheMapR using forcing from the PRISM dataset. Mean temperatures are shown for each month from 1991-2020.

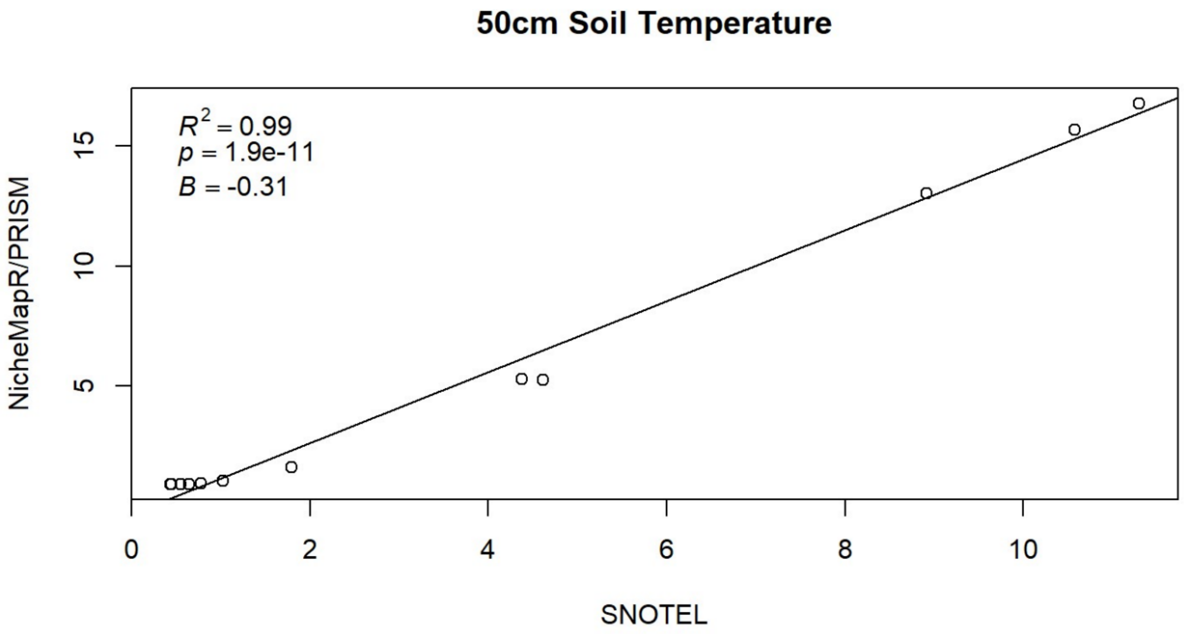


Fig. S7: Example regression output from predicted v. observed monthly average soil temperatures using NicheMapR with climate forcing from PRISM. Observed data from the Banner Summit SNOTEL (#312: Latitude: 44 deg; 18 min N; Longitude: 115 deg; 14 min W; Elevation: 7040 feet).

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